Secondary Representational Abilities in Nonhuman Primates (*Macaca nemestrina, Cebus apella*)

Annika Paukner

Department of Psychology

University of Stirling

Thesis submitted in fulfilment of the requirement for the degree of

Doctor of Philosophy

December 2005

05/06

Contents

Chapter 1 The Development of Representational Abilities in Human and Nonhuman Primates

Chapter 2 Self-Imitation in Pig-Tailed Macaques

Chapter 3 Imitation Recognition in Pig-Tailed Macaques and Capuchin Monkeys

Chapter 4 A Mark Test Assessing Mirror Self-Recognition in Pig-Tailed Macaques

Chapter 5 A Mirror Study with Capuchin Monkeys

Chapter 6 Means-Ends Reasoning in Capuchin Monkeys

Chapter 7 Secondary Representational Abilities in Monkeys – Evaluation and Future Directions

Acknowledgements

There are many people who contributed to this thesis in one way or another. I am deeply grateful to all of them.

Thanks to my supervisor Jim Anderson for letting me freely work on my own ideas, for useful comments and for letting me copy a fair part of his reference collection. Thanks to Hannah Buchannan-Smith, my second supervisor, for comments on data I presented, and to David Donaldson, substitute supervisor and postgraduate tutor, for teaching me to recognise bad academic writing. Thanks to the University of Stirling for a PhD studentship, and to the Japanese Ministry of Education, Culture, Science, Sports, and Technology (MEXT) for funding my study visit to Japan.

Thanks also to my host labs, who allowed me to work with their monkeys: Kyoto University, Parma University and the CNR Rome. Thanks to Kazuo Fujita, Giacomo Rizzolatti and Elisabetta Visalberghi for inviting me.

In Japan, thanks to Hika for helping me to work with the monkeys, and special thanks to Adachi, for dealing with the police when my apartment got burglared. Thanks to Helen for providing much needed social support. In Parma, I am most grateful to Pier Ferrari for making my research progress his personal project, and for pushing me further than I ever thought I could go. For all the fun times, thanks to Eleonora, Magali, Stefano, Caroline, Lisa, Abdel and Fabian. In Rome, thanks to Silvia for putting me up in her apartment, and to Diane and Carlotta for helping me to conduct the experiment.

Even though the data did not make it into the final thesis, I am still grateful to Keith Morris at the MRC Human Reproductive Science Unit in Edinburgh, for allowing me work with his monkeys. Thanks to all the staff there, Irene, Jim, Colin, Phil, Diane and later Dawn. Special thanks to Kev for fixing my apparatus when the stumpies ripped it apart.

Thanks also to all the technical staff everywhere: in Parma, thanks to Paolo for tolerating me in "his" monkey room, and to Fabricio for the daily smiles and chocolates. In Stirling, thanks to Bruce, Catriona, Stephen and Shona for technical support. Special thanks to Bob for copying all my video tapes, and to Srjan for fixing my computer. Thanks to all the secretaries – there have been so many changes in appointments over the last three years, I'm bound to forget someone, so here's a general thank you to you all.

Crucial social support in Stirling came from Corri, Alex, Kim, Clare, Inbal, Anita, Mairead, Sarah, Christine and Marina. For distractions, thanks to Roz and her ponies, to The Tracks and to the poker players. For just being there, thanks to Natalie, Anne, Corinna and Sara. I am also eternally grateful to Anne for proof-reading the whole thing.

Finally, thanks to my parents for letting me pursue my dreams. Your support allowed me to be where I am today. Most importantly, thanks to Richard, who always believed in me. I couldn't have done it without you.

Publications and Conference Presentations

Publications

Data presented in Chapter 5 have been published in: Paukner, A., Anderson, J. R. & Fujita, K. (2004). Reactions of capuchin monkeys (*Cebus apella*) to multiple mirrors. *Behavioural Processes, 66,* 1-6.

Data presented in Chapter 3 have been partly published in: Paukner, A., Anderson, J. R., Borelli, E., Visalberghi, E. & Ferrari, P. F. (2005). Macaques (*Macaca nemestrina*) recognise when they are being imitated. *Biology Letters, 1,* 219-222.

Data presented in Chapter 6 will be published in: Paukner, A., Anderson, J. R. & Fujita, K. (in press). Redundant food searches by capuchin monkeys (*Cebus apella*): a failure of metacognition? *Animal Cognition.*

Conference presentations

Paukner, A., Anderson, J. R., Borelli, E., Visalberghi, E. & Ferrari, P. F. (2005). Macaques recognise when they are being imitated. Talk presented at the SPRG Spring Meeting, *The Burn, January 2005.*

Paukner, A., Anderson, J. R., Borelli, E., Visalberghi, E. & Ferrari, P. F. (2005). Macaques recognise when they are being imitated. Talk presented at Animality! Personality in animals, *Stirling University, February 2005.*

Paukner, A., Anderson, J. R., Borelli, E., Visalberghi, E. & Ferrari, P. F. (2005). Macaques recognise when they are being imitated. Talk presented at PSGB Spring Meeting, *Chester, March 2005.*

Paukner, A., Anderson, J. R., Donaldson, D. I. & Ferrari, P. F. (2005). Cued repetition of self-directed actions in pigtailed macaques: evidence for episodic memory? Poster presented at the 1. Congress of the European Federation for Primatology, *Goettingen, August 2005.*

Paukner, A., Anderson, J. R., Donaldson, D. I. & Ferrari, P. F. (2005). Cued repetition of self-directed actions in pigtailed macaques: evidence for episodic memory? Poster presented at 46th Annual Meeting of the Psychonomic Society, *Toronto, November 2005.*

Abstract

As human infants mature, their cognitive operations achieve increasing levels of complexity, which is thought to be based on an increasing complexity of their mental representational abilities. Perner (1991) proposed three different types of mental representations that are believed to underlie this development: primary representations, which represent reality accurately and faithfully; secondary representations, which are 'detached' from immediate reality and therefore capable of modelling past or future situations; and metarepresentations, which explicitly represent the relationship between the representation and its content. Numerous studies have provided evidence that in humans, primary representations appear to be present from birth, secondary representations emerge between 1.5-2 years, and metarepresentations develop between 4.5-5 years.

Much less is known with regard to the phylogenetic development of representational abilities. Studies with nonhuman primates suggest the presence of primary and secondary representational abilities in great apes, but only primary representational abilities in monkeys. However, the current lack of evidence for secondary representational abilities in monkeys might be related to the limited number of studies addressing this issue and/or methodological limitations, thereby perhaps not reflecting a true negative.

In order to contribute towards a more complete picture of nonhuman primates' representational abilities, a series of studies was conducted to examine secondary representational abilities in two monkey species (*Macaca nemestrina, Cebus apella*). Pig-tailed macaques were tested for self-imitation, imitation recognition and mirror self-recognition; capuchin monkeys were tested for imitation recognition, mirror self-recognition and means-ends reasoning, all thought to be indicative of secondary representational abilities. Evidence for primary representations was found in both species, however none of the experiments provided strong evidence for secondary representational abilities. One possible exception is two pig-tailed macaques' responses to marks on their heads during a classic mark test for self-recognition, but since these responses consisted of mere swipes to their heads and not intensive mirror-mediated responding, this finding cannot be regarded as conclusive.

The absence of evidence for secondary representational abilities in monkeys in the present work therefore confirms previous research findings and may suggest that monkeys are limited to primary representational abilities. Replications and extensions of the present work are highly recommended and can significantly contribute to our understanding of the evolutionary origin of human and nonhuman primate cognition.

Chapter 1: The Development of Representational Abilities in Human and Nonhuman Primates

Chapter 1 defines the concept of a mental representation, and introduces Perner's (1991) classification system of representational complexity. Evidence is presented for primary, secondary and metarepresentational abilities in human infants and for primary and secondary representational abilities in great apes. Monkeys can be attributed with primary representational abilities but to date, evidence for secondary representational abilities is lacking. Addressing this gap in the literature, a program of study is outlined.

1.1. 'Mind' and psychology

The term 'mind' is experiencing a revival in the psychological community as evidenced by recent publications such as *Kinds of minds* (Dennett, 1996), *Wild minds* (Hauser, 2001) and *The mind made flesh* (Humphrey, 2002). Between the years of its initial abandonment following the behaviourist revolution and its comeback in recent years, substantial progress was made in defining what a 'mind' actually is. Cognitive psychology has identified and clarified several overlapping strands of 'mind' including memory, attention, language, categorisation, reasoning and deduction. Ultimately, cognitive psychology is pursuing the same question as philosophers going back to at least Aristotle: What is a mind, and how does it work? However, wary of the word 'mind' and its connotations with 'soul' or 'spirit', cognitive psychologists have often opted for terms like 'information processing', 'cognitive mechanism' or even 'high level functions'. Underlying all of these terms is the construct of 'mental representation'.

1.2. What is a representation?

A representation can be defined as "any notation or sign or set of symbols that stands for some thing in the absence of that thing" (Eysenck & Keane, 2000). Importantly, a representation (the set of symbols) must not be confused with the meaning or content of the representation. For example, considering the photograph of a monkey, the photograph (coloured dots on a piece of paper) is the representation, whereas the monkey is what is being represented. To avoid this confusion in the usage of the word representation, Perner (1991) distinguished between the representational medium, i.e. that which is the object representing another object (photograph), and the representational content, i.e. that which is being represented by the representational medium (monkey). Following Perner (1991), 'representation' is used hereafter to mean 'representational medium'.

Generally, representations can be categorised as either external or internal. External representations usually refer to external objects that represent something else, such as maps (representing an area), photographs and pictures (representing objects), and numerals (representing quantities). Thus, external representations are mostly notations, either written language or graphics. Internal representations on the other hand refer to representations 'inside one's mind', i.e. representing external objects internally and thereby enabling explicit thought and mental imagery (Eysenck & Keane, 2000). Internal representations are often thought of as 'pictures in the mind', but even without falling into Cartesian Dualism, the notion of 'internal pictures' is not useful and raises many conceptual problems (such as the homunculus problem; von Eckhardt, 1999). A better concept realisation of internal representations was proposed by Armstrong (1968) and his "mind-brain identity theory", which holds that mental representations are realised through distinct neural patterns in the brain. Mainstream psychology quickly adopted this model of internal representations, and it has generated a wealth of information clarifying internal representations' function and usage. Internal representations are also called mental representations, and this term will be used in the following.

1.3. Explicit and implicit mental representations

Mental representations can be further classified as either implicit or explicit. Put simply, explicit representations are the 'pictures in the mind' which we use in our conscious thoughts, whereas implicit representations are the ones we are not aware of, but that are nonetheless underlying cognitive processes. More generally, the implicit/explicit distinction has been based on the extent to which the representational content is accessible to other cognitive sub-systems. For example, Karmiloff-Smith (1986) defined implicit representations as being largely inaccessible to other cognitive systems and explicit representation as being accessible to other cognitive systems. In particular, conscious or verbal access to the representation is usually taken as an indicator that the representation is explicit (Dennett, 1978). However, all knowledge must be accessible to some system to be evaluated as 'knowledge', so that accessibility is not suitable as the sole criterion for the implicit/explicit distinction. Schacter (1987) suggested that implicit representations derive from previous experiences with, or exposure to, a stimulus, which leads to an increase in cognitive activity in the absence of conscious or intentional recollection. In contrast, explicit representations are thought to be conscious and intentionally accessible to other cognitive systems (e.g. hypothetical reasoning, evaluation of truth; Dienes & Perner, 1999). As such, processes of conditioning, non-associative learning and priming, which often occur without conscious processing, can be explained in terms of underlying implicit representations whereas any form of conscious processing is more likely based on explicit representations.

Of course, if explicit representations are defined as being accessible to conscious thought and verbal processing, then by definition animals and pre-verbal human infants cannot be judged to possess explicit mental representations because they lack the necessary verbal skills. This conclusion may be erroneous, however, given recent evidence of representational abilities even in human neonates (see below). Tracing the development of representational abilities informs us not only about the ontogenetic origin and development of intentional conscious thought, it might also give us some idea of how explicit representations evolved, and what precursors to human representational abilities may be found in other animals.

1.4. Classification of explicit mental representations

Mental representations can be conceived at different levels of complexity, which has led to different classification systems of mental representations. Leslie (1987) suggested that accurate, faithful and literal representations of concurrent reality are captured by *primary representations*. Due to their direct semantic relation to the world (i.e., they represent what is 'out there' and only what is 'out there'), these primary representations appear to be fundamental to accurate reality monitoring, and therefore crucial to survival and successful reproduction. For example, it would be vitally important to recognise and represent a predator such as leopard accurately in order to respond with the appropriate behavioural response (which might be flight to the treetops). If a leopard was represented as an eagle (triggering the behavioural response of flight to the ground), or even worse, as a conspecific (triggering an approach response) or a stone (triggering no further response), an individual would significantly lower its chances of survival. However, primary representations do not always represent external reality accurately and faithfully; perceptual or conceptual errors may occur, especially if the external object is camouflaged or otherwise ambiguous in its interpretation. However, assuming that the perceptual and cognitive system is capable of identifying external objects accurately, primary representations serve the purpose of representing external reality as it is.

The concept of primary representations appears to be generally undisputed. Perner (1991) described primary representing individuals as holding a single updating model of reality, which is not modality specific and capable of temporally extending beyond immediate present reality. As such, individuals might be quite capable of operating on primary representations alone. However, one of the major limitations of primary representations is that temporal change cannot be accurately represented. That is, should new information be obtained that is incompatible with previously acquired primary representations, then the old representations are simply 'erased' and replaced by the new information. It is therefore not possible for primary representational individuals to track changes over time, or to retrace any steps taken (Perner, 1991).

These difficulties can be overcome through the use of what Perner (1991) called *secondary representations*. Secondary representations are representations of past, future or entirely hypothetical situations that are "decoupled" (Leslie, 1987) or "detached" (Gaerdenfors, 1996) from the immediate external environment. The important difference between primary and secondary representations is that primary representations necessarily model the present state of affairs, but secondary representations can go beyond the present situation and can be flexibly adapted to different purposes. So for example, while holding a banana in her hand and perceiving the banana as a banana (primary representation), a child using secondary representations is at the same time capable of pretending that the banana is a telephone (secondary representation; Perner, 1991). Secondary representations are thought to be held alongside primary representations and in fact are dependent on primary representations, i.e. an organism without primary representational capacities would not be able to hold secondary representations.

The final step in representational abilities in humans concerns *metarepresentations* (Perner, 1991). According to Perner (1991), metarepresentations not only represent other representations, but crucially represent the representational relation itself, i.e. a metarepresentation is a "representation of a representation as a representation" (pp. 35, emphasis in original). For example, while the Mona Lisa is a representation of the wife of Francesco del Giocondo, a photograph of the Mona Lisa is a metarepresentation because it is a representation of the representation of the wife of Francesco del Giocondo. An individual capable of metarepresentations can appreciate this representational relationship, and will understand not only the causal relationship between the representational media (photograph representing painting representing woman), but also appreciate that subsequent changes to the representation (say, restoration of the Mona Lisa leading to brighter colours in the painting) will make the previously captured metarepresentation invalid (as it does not capture the present state of the representational medium anymore). This crucial evaluation of representational relations allows individuals to make judgements about the accuracy of other individual's mental content (perceived as representations), which can only be achieved through the use of metarepresentations. That is, individuals must come to understand that other individuals represent reality, but that occasionally reality may change so that individuals may hold false beliefs. Indeed in the human psychological literature, passing false belief tests (being able to make a judgement that what others believe is not true) has become the litmus test for metarepresentational abilities (Perner, 1991).

1.5. The development of representational abilities in human infants

As metarepresentations are dependent on secondary representations and secondary representations are dependent on primary representations, the development of increasingly complex representational abilities can be traced throughout childhood using distinct behaviours as markers of representational abilities.

1.5.1. Primary representations

In humans, primary representations appear to be present from birth (Perner, 1991). For example, Meltzoff & Moore (1977) showed that neonates as young as 1h can engage in facial imitation, i.e. reproduce facial actions of an adult model, even though they cannot see their own facial features. In other words, neonates can transform the visual input of a facial gesture into identical kinaesthetic output, thus apparently forming an amodal representation of the facial action. In addition, facial imitation can occur after extended delays, indicating that the infant is not stimulus-bound to appropriate external factors, but has formed a representation of the previously perceived actions. Although neonatal facial imitation is disputed (e.g. Anisfeld et al., 2001), at least one action (tongue protrusion) appears to be robustly copied by human infants (Anisfeld, 1996; Meltzoff & Gopnik, 1989).

Other indicators of infants' primary representational abilities come from studies of object permanence. For example, in visible displacement tasks (also called A-not-B-error task), an infant is shown an attractive toy which is hidden under a lid or container at location A, and subsequently allowed to retrieve the toy from its hiding location. This process is repeated several times. If the toy is then moved from one hiding place (A) to another (B), infants aged 8-12 months will look significantly longer at the actual hiding location (B), yet reach for the previous hiding location (A) (Hofstadter & Reznick, 1996). The difficulty in retrieving the toy from its new hiding location has been related to difficulties in inhibiting previously reinforced action sequences (e.g. Smith & Thelen, 2003), yet the infant's eye gaze suggests that by the age of 8-12 months, infants nonetheless know the true location of the toy. Correct task performance appears to be based on primary representations in that the toy is represented even though it is not directly visually perceived anymore.

Perner's concept of primary representations is quite different from Piaget's (1954) concept of sensorimotor schemes. According to Piaget, children first form mental representations (schemas) through accidental discovery of effects, which are then purposefully repeated until the infant becomes proficient at producing the desired effect (primary circular reactions). New experiences are assimilated into already existing schemas (using an old scheme for interpreting a new experience), while at the same time already existing schemas may be accommodated to new experiential demands (adapting an old schema for a new experience). Initially, schemas are perceptually evoked, which leaves infants 'stimulus bound' i.e. restricted to object understanding only within each specific modality that the object has been experienced in. Only later, at about 8-12 months, different modalities are integrated to form a complete representation of an object (co-ordination of secondary circular actions; Piaget, 1954). There are two striking differences between the two theories: Piaget viewed mental representational abilities of infants <1year as restricted to present reality and modality-specific, whereas Perner attributes infants <1year with amodal representational abilities beyond the immediate present. Evidence from deferred neonatal facial imitation and object permanence studies (using expectation violation procedures) appear to support Perner's theory.

1.5.2. Secondary representations

Between 1.5-2 years of age, secondary representations appear to emerge in children, i.e. children progress from a single updating model of reality to being able to entertain multiple models. The most thoroughly studied phenomenon indicative of secondary representations is probably pretend play. Other indicators of secondary representational abilities include an understanding of invisible displacement and external representations, attribution of emotions and intentions, means-ends reasoning, mirror self-recognition and synchronous imitation (Perner, 1991; Suddendorf & Whiten, 2001).

Pretend play involves pretending that an object stands for another object, or to pretend the presence of an object in its absence. Even though some have argued that pretend play involves metarepresentational abilities because the pretender has to represent both the actual object and another's counterfactual representation (e.g. Leslie, 1987), this assumption has been questioned. As Perner (1991) argues, pretend play can be achieved on the basis of secondary representations alone by representing the actual object (primary representation) alongside the pretended object representation (secondary representation), which is tagged as "pretend" in order to avoid reality confusions (see also Jarrold, Carruthers, Smith & Boucher, 1994). Indeed, children appear well capable of differentiating real objects from pretend objects; not many children actually eat their own mud cakes.

Pretend play dramatically increases in complexity between 1.5-3 years of age. In early pretend play, children only use realistic objects e.g. an empty cup that they pretend to drink from. At around 2 years, children can use unrealistic objects, e.g. a wooden block as a telephone receiver, and at around 3 years, children can engage in pretend play without the aid of any objects (Corrigan, 1987; O'Reilly, 1995). Apart from an increase in diversity of objects used, children also engage in more and more elaborate forms of pretend play and involve others in the pretend situation (e.g. Howes & Matheson, 1992). Children only come to understand that pretending is also a mental activity at a later stage (4 years onwards), when metarepresentations are established (Jarrold et al., 1994).

Another indicator of secondary representational abilities is passing Piaget's (1954) hidden (or invisible) displacement tasks. Invisible displacement tasks involve an object hidden in a small container, which is moved inside a bigger container. When the small container re-emerges, it is empty. For a mind capable of only primary representations, the disappeared object is a puzzle. Primary representations are only capable of processing a single updating model of reality, and are therefore incapable of reasoning about the location of the object. With secondary representations, however, an individual can hold in mind the present situation ("present: small container empty"; primary representation) and the past situation ("past: small container in large container"; secondary representation), which allows reasoning about the object's likely present location (in the larger container; Perner, 1991). At 1.5 years, most infants will pass such invisible displacement tasks (Haake & Somerville, 1985).

Similarly, means-end reasoning is argued to be reliant on secondary representational abilities because the present problem state (primary representation) needs to be co-ordinated with a desired future solution state (processed as secondary representations), and the necessary steps from the problem state to the solution state need to be found (Perner, 1991; also Piaget, 1954). Mentally constructing solutions to problems is also thought to underlie insight (Piaget, 1952), i.e. the appearance of a sudden solution to a problem without explicit behavioural attempts to solve the problem. Evidence for goal expectations in young infants comes from experiments by Bullock & Lutkenhaus (1988). These authors asked 17-26 month-old infants to engage in three distinct tasks with clearly defined goals or outcomes. For example, children were shown a picture of a house made of three wooden blocks and were asked to build this house from a pile of relevant and irrelevant building blocks. At 17 months, infants rarely pursued the required goal; at 20 months, infants worked towards the desired goal but did not fully achieve it, whereas at 26 months, most children not only achieved the desired goal but also engaged in monitoring, correcting and controlling goal-directed actions. For example, children would smile and say "Done!" whenever a task was completed, which is a clear indicator that the children were aware of the goals of their own actions. Similarly, Kagan (1981) found negative reactions to unsuccessful achievements in 20 month-old children.

Understanding external representations (such as pictures, photographs, films) also requires the ability to process secondary representations. Perner (1991) suggested that in order to understand a photograph, a primary representation (e.g. Daddy on the couch) needs to be co-ordinated with a secondary representation (e.g. Daddy at the beach on the picture), which can be achieved by labelling the photographic Daddy as pictorial (i.e. in the picture). This way, no reality confusion between the 'real' Daddy and the pictorial Daddy can occur. Even though 5 month-old children already recognise the resemblance between a person and a picture of that person (Dirks & Gibson, 1977), it is not until they are about 2 years that children actually show an interest in pictures. At 1 year, children treat pictures as little more than coloured pieces of paper (Perner, 1991). Furthermore, DeLoache (1991) showed that 2.5-year-old children can judge pictures of a room to be either similar or dissimilar to the actual room. It is not until age 3 that children can use a picture or a model of the room as a source of information to find hidden objects in the actual room (DeLoache, 1987). Even at that age, the understanding of the pictured room is restricted and is not understood metarepresentationally, i.e. children do not interpret the picture as a representation of the actual room. This step in development is only reached by ca. age 4, when the representational relation between the room and its picture becomes explicit (Perner, 1991).

Related to picture and photographic understanding is mirror-self recognition. Mirrors are ambiguous objects; they reflect their immediate surroundings accurately, faithfully and three-dimensionally, and even duplicate movements in real time, yet the image remains on the surface of the mirror itself. Thus, a mirror can be seen as a particular type of picture or image that might more easily be mistaken to contain the objects it reflects due to its naturalistic representation including movements. Understanding mirrors as reflecting external objects, and particularly understanding reflections of oneself as just that – reflections of oneself – are thought to depend on secondary representations for the same reasons that external picture understanding is built on secondary representations. To understand that a mirror reflects an object, one has to understand that the same object cannot be in the two different places at the same time, i.e. in the external environment and in the mirror.

The solution involves forming a secondary representation of the external object ("Daddy in mirror"), which can then be held alongside the primary representation of the object

("Daddy on couch"). As for self-recognition, children would need to co-ordinate the primary representations of themselves with the secondary representation of themselves in the mirror (Perner, 1991; Asendorpf & Baudonniere, 1993). Mirror self-recognition can be observed by 1.5-2 years in infants (Amsterdam, 1972), by initially exposing infants to mirrors, observing spontaneous appropriate mirror-mediated self-directed behaviours and then applying a spot of rouge onto the infants' faces without their knowledge. If infants recognise themselves, they might try to touch the mark on themselves rather than on the mirror. This type of behaviour is thought to be brought about by comparisons of the present image with rouge mark ("me-now") with a secondary representational concept of oneself prior to the rouge spot ("me-past"; Suddendorf, 1999). Prior to recognising themselves, children appear to perceive the representation of themselves to be another child, directing smiles or vocalisations to it, or trying to engage the 'other' child in play activities (Amsterdam, 1972).

Attributing emotions and intentions to others may also involve secondary representational ability (Perner, 1991). For example, one way of successfully attributing emotions to others may be by simulating a hypothetical situation involving oneself ("How would I feel in that situation?"). Thus, the primary representation of oneself (me-now) needs to be held alongside the hypothetical situation (me-as if). Children during their second year of life show empathic behaviour (indicating their understanding of others' pleasure or distress) by e.g. directing comforting behaviour towards others in distress (Zahn-Waxler, Radke-Yarrow & King, 1979).

Perner (1991) argued for infants' understanding of others' intentions as a secondary representational ability, not a metarepresentational ability, i.e. that children need to combine the person's present behaviour (primary representation) with the intended/anticipated goal of the action (secondary representation). A detailed appreciation of the person's mental states in terms of representing the desired goal is not required; these abilities only emerge at 4-4.5 years with metarepresentational capacities, but are not crucial in order to appreciate that others' actions are guided by goals. Meltzoff (1995) found that at 1.5 years, infants copy an experimenter's goal of an action even when this goal has not been directly presented to them. In contrast, infants are far less likely to perform the same goal if the goal-directed action was performed but not achieved by an inanimate machine. However, below 4 years of age, infants' secondary representational understanding of intentions is rather limited. For example, younger infants do not appear to appreciate that a desired outcome can either be achieved deliberately or accidentally. Astington (1993) told a story about two girls to children aged 3-5 years: one girl threw bread crumbs on the floor, the other dropped bread crumbs on the floor. In both cases, birds came and ate the crumbs. When asked which girl meant to feed the birds, 3-year-olds were equally likely to pick either girl, whereas 4- and 5-year-olds were significantly more likely to choose the girl that threw the crumbs. Thus, children seem capable of appreciating intention as an internal state that can be distinguished from overt behaviours only with metarepresentational abilities (however, see Tomasello & Barton (1994) for evidence that 24 month old children learn novel words for intentional but not accidental contexts, which suggests that intentionality as an internal concept may be understood earlier in life).

Even though Perner (1991) did not make a case for imitation understanding as a secondary representational ability, Whiten (1996) and Suddendorf & Whiten (2001) argued that secondary representational abilities may also underlie synchronic imitation and imitation recognition abilities. Synchronic imitation involves two individuals engaging in the same activity using identical objects. These activities do not have to be identical or directly imitative of each other, but individuals look at each other regularly and appear to realise the correspondence between themselves and the partner as indicated by positive mood and simultaneous beginning and ending of activities or changing of objects (Asendorpf, Warkentin & Baudonniere, 1996). Thus, synchronic imitation involves a recognition of imitative intentions, and actively seeking out imitative correspondence between own and other actions, which can be achieved by conceiving of the other person's intention to imitate (Suddendorf & Whiten, 2001). More direct evidence for recognition of intentional imitation comes from experiments by Meltzoff (1990; 1996). Meltzoff presented infants aged 14 months and above with two experimenters: one imitating the infants' object-directed actions, the other simultaneously performing a different action towards an identical object. Results showed that infants not only looked longer at the imitating experimenter, but also directed more social responses (smiling, vocalisations) and testing of the behavioural contingency at the imitator, indicating an understanding of the imitator's intentions to imitate themselves (Nadel, 2002).

1.5.3. Metarepresentations

The last step of representational development in humans is the ability to form metarepresentations. Metarepresentations are representations that include representational relations (Pylyshyn, 1978). For example, in order to understand a photograph metarepresentationally, one has to represent the photograph itself (as a coloured piece of paper), what the photograph depicts (Daddy at the beach) and importantly, links between the photograph itself and its content, i.e. how the depicted object relates to the photograph (Perner, 1991). Metarepresentations thus not only permit the formation of mental models, they also enable individuals to think of other individuals as representing entities. Beliefs become not mere reflections, but interpretations of reality. Being able to interpret thoughts and beliefs furthermore allows an evaluation of these mental activities, i.e. whether what others think or believe is true or false. This ability becomes apparent when children start to pass false belief tasks. For example, in the classic false belief task (e.g. Baron-Cohen, Leslie & Frith, 1985), children are told a story in which one character, Sally, places a marble into a basket, and then leaves the room. A second character, Anne, takes the marble from the basket and places it into a box. When Sally returns, children are asked where Sally will look for her marble. Children who can appreciate that Sally's belief about the marble's location is dependent on the information available to Sally, answer that Sally will look into the basket. This answer requires metarepresentational abilities in that another person's representations (belief about object location) are evaluated according to what the person is capable of representing (i.e., the marble location according to Sally's best knowledge). Failure to understand the relationship between a representation (belief) and the circumstances that prompt a belief (marble location) will result in a failure to accurately model the other person's belief. That is, without metarepresentational abilities, children cannot appreciate that Sally is holding a false belief (that Sally cannot know where the marble has been transferred to), and say that Sally will look for the marble in the marble's actual location (box). Answering with the marble's actual location is typical of 3-year-olds, whereas around 4.5 years, children come to pass such false belief tests (Wimmer & Perner, 1983). A widely-used term for metarepresenting others' mental states is also Theory of Mind (TOM; Premack & Woodruff, 1978; Wimmer & Perner, 1983).

Other achievements relying on metarepresentations and emerging around 4-4.5 years include the ability to distinguish appearance from reality, episodic memory/source memory, and an understanding of desire as an internal representation (Perner, 1991;

Suddendorf, 1999). Flavell, Flavell & Green (1983) first studied appearance-reality distinctions by showing children a sponge that looked like a piece of rock. At first, most children reported that they thought it was a rock; they were then allowed to handle the object. Finally, an experimenter asked them two questions: what is this object, and what does it look like? At 3 years, most children answered that the object is a sponge and looked like a sponge, failing to appreciate that a person who has not manually explored the object would be unable to come to this conclusion based on visual inspection alone. In contrast, most 4-year-olds answered that the object looks like a rock but actually is a sponge, thereby showing an appreciation of others' access to representational information.

Both episodic memory and source monitoring abilities require metarepresentational thought, and they emerge in children at around 4 years of age. Episodic memory is defined as a form of declarative, long-term memory, which is characterised by a "re-living" of, or "mental time-travel" to, the past event (Tulving, 1972). Episodic memories thus require metarepresentational abilities because not only are secondary representations involved in episodic memories of the past event, these secondary representations are also judged as personally experienced past events (Perner, 1990, 1991, 2001). In other words, the relation between the memory of the event and the event itself is explicitly represented. Evidence suggests that children generally are not able to remember episodes prior to at least 3-4 years of age ('childhood amnesia'; Perner & Ruffman, 1995). Similarly, source monitoring refers to the ability to know the origins of one's own knowledge. For example, Wimmer, Hogrefe & Perner (1988) either showed children an object that was put inside a box, or simply told children what object was put inside the box. Children were then asked what object was put inside the box, and crucially, how did they know? Even though all children could name the correct object, most 3-year-olds failed to accurately report on how they knew the answer, whereas most of 4-year-olds specified that they either saw or were told about the object. Source monitoring is similar to episodic memory in that the relationship between the past event and the memory of that event is explicitly represented, however source monitoring does not strictly require a 're-living' of the past event.

A final achievement based on metarepresentational abilities that will be discussed here is the understanding of desire as an internal representation. Although a child capable of only secondary representations can conceive of others as having desires, she is restricted in this conception in that she cannot appreciate that the other person is representing the object of desire, which might be different from her own desires. Moore et al. (1995) showed that if a person has conflicting desires with children's own desires, 5-year-olds, but not 3-year olds, can appreciate that the other person desires a different object (see also Gopnik & Seager, 1988; cited in Astington & Gopnik, 1991).

1.6. Adaptive significance of secondary representations and metarepresentations

As outlined above, children go through a series of mental representational developments ranging from primary representations, probably present at birth, secondary representations, emerging at 1.5-2 years, and finally metarepresentations, emerging at 4-4.5 years. From an evolutionary perspective, the adaptive significance of advanced mental representations might be questioned. While the adaptive advantage of primary representations appears quite straight forward (to accurately monitor one's own surrounding), the functions of secondary and metarepresentations may seem less clear.

Suddendorf & Whiten (2001) suggested that secondary representations allow the conception of alternative situations (past, present or future) and therefore permit simple future planning abilities. Individuals with even simple planning abilities would be able to anticipate the consequences of their own actions and thereby become "Popperian creatures, since, as the philosopher Karl Popper once elegantly put it, this design enhancement 'permits our hypotheses to die in our stead'." (Dennett, 1996, pp. 116). Understanding others' intentions and emotions (based on secondary representations) might similarly facilitate predictions of other individuals' reactions and behaviours.

The development of metarepresentations might further enhance an individual's understanding of the causes of others' behaviour, and thereby increase the predictive power of individuals. Furthermore, the appreciation that others hold representational content and might be susceptible to false beliefs could promote the exploitation of these false beliefs. In other words, individuals might deceive others for their own benefit, thereby gaining a significant competitive advantage. This "Machiavellian intelligence hypothesis" (Byrne & Whiten, 1988) is based on previous social intelligence hypotheses (e.g. Jolly, 1966; Humphrey, 1976); together they postulate that human advanced intellectual functions are the result of increasing social group size and complexity, requiring adequate means to keep track of, monitor and manipulate others' social relationships with each other.

A different function for metarepresentational abilities was proposed by Suddendorf & Corballis (1997), who suggest that 'mental time-travel' to a past event (characteristic of episodic memory, which is based on metarepresentations) might also be turned into 'mental time-travel' into possible future events, thus allowing more elaborate future planning abilities. In particular, simple planning abilities concerning future situations, as afforded by secondary representation, would be superseded by representations of future needs and drives, which cannot be modelled by secondary representations alone because future needs imply representations of intentionality outside of the present context (Suddendorf, 1999). The notion that metarepresentations make 'mental time-travel' into the future possible has also been called the "Bischof-Koehler hypothesis" (Suddendorf, 1999).

Another hypothesised function of metarepresentational abilities is concerned with increased self-control following the symbolic representation of rewards (Suddendorf, 1999). The symbolic representation of immediate and delayed rewards might help individuals to disengage from present needs and drives, and help to facilitate a self-controlled rather than stimulus-controlled conduct. Indeed, by age 4, children can forego a smaller, immediate reward in favour of a larger but delayed reward (Mischel, Shoda & Rodriguez, 1989). Other research has shown that by focusing on abstract properties of a reward, self-control (delay of gratification) increases, whereas focusing on the consummatory properties of food rewards decreases self-control (Mischel & Mischel, 1977). In other words, primary representations of positive consequences may reduce self-control whereas secondary and metarepresentations of positive consequences may increase self-control.

A related advantage influenced by symbolic understanding may be linguistic abilities. Alternatively, perhaps linguistic abilities prompted metarepresentational abilities – we do not know the causal connection between these two processes (Suddendorf, 1999). Language is present in children before metarepresentations emerge, yet correlations have been found between linguistic abilities and passing false belief tests (Astington & Jenkins, 1999). A symbolic understanding of language might lead to improved communication and comprehension, and furthermore facilitate generalisation of concepts and behaviours (Suddendorf, 1999).

1.7. Representational abilities in apes

Given the potential adaptive value of secondary and metarepresentations, it appears that almost any individual might benefit (i.e. increase its reproductive fitness) from advanced planning and self-control abilities. It is thus not unreasonable to assume that other animals might also possess secondary or metarepresentational abilities. A good starting point for comparative investigations on this issue is the great ape clade, comprising chimpanzees, bonobos, gorillas and orang-utans. Great apes, and chimpanzees in particular, are the evolutionary closest living species to humans, and therefore appear most likely to possess similar mental abilities. Similarities in mental processes may have arrived via two different routes: either by homology, i.e. a common ancestor developed advanced representational abilities which were retained after the split into human and nonhuman primates; or by analogy, i.e. similar ecological or social selective pressures stimulated a development of similar or identical features independently in both groups (Suddendorf & Whiten, 2001). Since great apes (henceforth: apes) also share with humans complex social group structures, both arguments appear plausible. By examining representational abilities in primates, it may be possible to outline the similarities of mental processes and possibly to determine whether our modern mental abilities stem from a common or a human-specific development. The following describes behaviours indicative of representational abilities in apes, focusing mostly on chimpanzees not only because chimpanzees are the closest living link to humans, but also because data on chimpanzees are more comprehensive than those relating to other nonhuman apes.

1.7.1. Primary representations

Evidence for primary representations is available from several strands of research. Neonatal chimpanzees (< 7 days) have been shown to copy facial acts (mouth opening and tongue protrusion) accurately enough to be recognised by independent observers (Bard & Russell, 1999; Myowa-Yamakoshi, Masaki, Masayuki & Matsuzawa, 2004; Tomonaga et al., 2004). Cross-modal matching (usually haptic-visual matching) has also been demonstrated in adult apes (Davenport, 1976), which is indicative of primary representations. Further evidence comes from studies showing that apes pass visible displacement (A-not-B) tasks (e.g. chimpanzees: Poti & Spinozzi, 1994; gorilla: Natale, Antinucci, Spinozzi & Poti, 1986).

1.7.2. Secondary representations

Suddendorf & Whiten (2001) comprehensively reviewed the literature for secondary representational abilities in apes, concluding that "probably all great apes [...] can entertain secondary representations." (pp. 640). The following gives a brief summary of the available evidence.

Invisible displacement (Piagetian object permanence stage 6) has been found in both chimpanzees and orang-utans (Call, 2001). Both species perform significantly above chance when the displacement has been to another adjacent container rather than to a non-adjacent container, however children aged 19-26 months make similar mistakes with regard to non-adjacent displacements (Call, 2001). As with visible displacements, difficulties in passing this task have been linked to inhibitory control restrictions (Diamond, 1991) rather than to memory deficits (de Blois, Novak & Bond, 1998).

Means-end reasoning in primates has mostly been studied in tool-using contexts, and focuses on the causal understanding of tools and their effects on the environment. Despite some inconsistent findings and individual differences, apes generally seem capable of keeping a goal state in mind whilst working through a subset of goals (Dunbar, 2000; Visalberghi, Fragaszy & Savage-Rumbaugh, 1995; see also Suddendorf & Whiten, 2001, for more examples).

There is also clear evidence that all great ape species pass mirror self-recognition tasks as assessed by Gallup's (1970) mark test (e.g. Gallup, 1970; Patterson & Cohn, 1994; Suarez & Gallup, 1981), however not all individuals pass this test consistently (de Veer, Gallup, Theall, van den Bos & Povinelli, 2003; Lethmate & Ducker, 1973; Swartz & Evans, 1991; Povinelli, Rulf, Landau & Bierschwale, 1993; Suarez & Gallup, 1981). Chimpanzees also have some appreciation of external representations as models of reality in that they can use a scale model to find hidden food in a real-life location (Kuhlmeier, Boysen & Mukobi, 1999), and can use Arabic numerals as representations for quantities (Matsuzawa, 1985; Boysen & Berntson, 1995).

Much research has been devoted to the extent to which apes are capable of imitating others. Even though synchronic imitation has not been observed to date, apes show a clear understanding of the concept of imitation. For example, when asked to repeat an experimenter's actions using a "Do this!" command, chimpanzees (Hayes & Hayes, 1952; Custance & Bard, 1994; Custance, Whiten & Bard, 1995) and a orang-utan (Miles, Mitchell & Harper, 1996) can replicate novel self- and object-directed actions (however, see Chapter 2 for a detailed discussion on how this form of imitation relates to representational abilities. See also Yunger & Bjorklund (2004) for failure to find generalised imitation in two orang-utans and Russon (1996) for failure to find deferred imitation in orang-utans). Furthermore, a chimpanzee has shown evidence of imitation recognition by directing more testing behaviours at an imitator rather than non-imitator (Nielsen, Collier-Baker, Davis & Suddendorf, 2004).

Far less evidence can be found for the attribution of intentions and emotions or on pretend play in apes, perhaps due to difficulties in assessing these phenomena experimentally in non-verbal species. Nonetheless, some experimental and observational evidence is available. Call & Tomasello (1998) report that both chimpanzees and orang-utans preferentially select a container that has been marked intentionally over one marked accidentally by an experimenter, showing at least a discrimination between these actions. An understanding of emotions may be inferred from field observations of chimpanzees comforting and consoling other individuals (e.g. Goodall, 1986; de Waal & Aureli, 1996; Aureli & de Waal, 2000). Observations have also been made of pretend play activities in chimpanzees, e.g. Vicki appeared to pull an imaginary toy (Hayes, 1951), and a wild chimpanzee appeared to treat a wooden log as if it was an infant (Wrangham & Peterson, 1996).

1.7.3. Metarepresentations

If, as suggested by the evidence presented above, apes can be judged to posses secondary representational abilities, can they perhaps also be judged to possess metarepresentational abilities? Evidence for metarepresentational thought in children has been assessed through false belief, appearance-reality and episodic memory tasks. Although there are no reported studies on appearance-reality assessments, there are experiments assessing apes' false belief understanding and episodic memory.

Call & Tomasello (1999) developed a false belief task not reliant on verbal abilities, and assessed chimpanzees, orang-utans and 4-5 year old children. Subjects watched an experimenter hiding a food reward (or a sticker for children) in one of two containers. A second experimenter then placed a marker on top of the baited container, and subjects were allowed to choose one container. If it was the baited container, they received the reward. In the crucial false belief condition, the experimenter left the room before placing the marker, and in his absence, a third experimenter switched the two containers' locations. When the first experimenter returned, he placed the marker on one container and subjects were allowed to respond. An appreciation that the second experimenter represented the reward location before the containers were switched, and therefore now held a false belief, would lead to the preferential selection of the now non-marked container. Five-year-old children selected the baited (and non-marked) container significantly above chance in this condition whereas 4-year-old children and apes failed the test (4-year-olds selected containers randomly, apes selected the marked container significantly above chance).

There have also been attempts to test episodic memory in apes, notably by Menzel (1999) and Schwartz, Colon, Sanchez, Rodriguez & Evans (2002). Schwartz and colleagues presented an adult male gorilla with three novel situations (novel or familiar person engaging in a novel action or manipulating a novel object), and after a 10 minute retention interval, gave three pictures to the gorilla showing either the previously observed situation or two distractor images. The gorilla's task was to return the picture of the previously witnessed situation. The gorilla's performance overall was low on this task, and although he returned appropriate pictures, the extent to which his performance relies on episodic memory remains questionable (see Chapter 2 for a discussion on the suitability of recognition paradigms for studying episodic memory).

Menzel (1999) tested a lexigram-trained chimpanzee in an unprompted recall and possibly episodic memory task. The chimpanzee witnessed a trainer hiding a food reward or object outside of the chimpanzee's outside enclosure. No other trainer was informed when or where an object was hidden, or even what the object was. It was then up to the chimpanzee to alert trainers to the presence of the object, and to direct them to the correct location. The chimpanzee succeeded in using lexigrams of the appropriate objects and the hiding places. Importantly, the chimpanzee alerted trainers after extended periods of delay (up to 16h) and in the absence of visual contact with the hiding location (see Chapter 2 for a more detailed discussion). However, how far communication of this sort requires episodic memory is not clear, as successful performance may not necessarily involve an autonoetic re-experiencing of the past event. Taken together, the presented evidence for metarepresentational abilities in apes appears weak (see also Suddendorf & Whiten, 2001; Parker & McKinney, 1999).

1.8. Representational abilities in monkeys

Looking further back along the evolutionary tree, monkeys shared a common ancestor with apes ca. 40-20 million years ago (Tomasello & Call, 1997). Monkeys also live in social groups, and therefore have been subjected to the same evolutionary pressures as apes and humans. It appears that like apes, monkeys would benefit from advanced representational abilities. Below, the evidence supporting this assumption is briefly reviewed.

1.8.1. Primary representations

Monkeys reliably pass visible displacement (A-not-B) tasks (e.g. Dumas & Brunet, 1994; Antinucci, Spinozzi, Visalberghi & Volterra, 1982, cited in Tomasello & Call, 1997; de Blois & Novak, 1994), indicative of primary representational abilities. Furthermore, infant rhesus macaques may imitate facial gestures, at least with regards to mouth and tongue movements (Ferrari et al., in prep). Both lines of research suggest primary representational abilities in monkeys.

1.8.2. Secondary representations

Less research has been conducted on secondary representational abilities in monkeys, and the data that have been obtained on this issue are largely negative. For example, De Blois & Novak (1994) and Dumas & Brunet (1994) found negative results on invisible displacement tasks in rhesus macaques and capuchin monkeys respectively (see also Mendes & Huber, 2004, for inconsistent results on an object permanence task in marmosets). However, Fillion, Washburn & Gulledge (1996) report successful invisible displacements by rhesus monkeys in a computerised task tracing hidden movements. In terms of mean-ends reasoning, Visalberghi and colleagues have extensively studied tool use and tool use understanding in capuchin monkeys. They concluded that even though capuchins are enthusiastic and proficient tool users, these monkeys succeed mostly on the basis of trial-and-error learning, not mental modelling of the problem situation (Visalberghi & Limongelli, 1994; see also Fragaszy, Visalberghi & Fedigan, 2004).

Studies examining pictorial understanding or mirror self-recognition in monkey species have similarly yielded negative results. Numerous monkeys species have been subjected to the classic mark test, including capuchin monkeys (e.g. Anderson & Roeder, 1989), long-tailed macaques (e.g. Mitchell & Anderson, 1993), rhesus macaques (e.g. Gallup, Wallnau

& Suarez, 1980) and olive baboons (e.g. Benhar, Carlton & Samuel, 1975). However, no monkey to date has convincingly passed the mark test or has shown robust spontaneous mirror-mediated self-exploration. Studies examining picture or photographic understanding in monkeys found that monkeys often appear to confuse the picture with the actual object rather than process the picture representationally (Bovet & Vauclair, 1998; Fagot, Martin-Malivel & Depy, 1999).

Imitative abilities have also been examined in monkeys, but no strong evidence of imitation has been reported. Two reported attempts to assess monkeys' conceptual understanding of imitation can be found in the literature, one by Mitchell & Anderson (1993) testing a pig-tailed macaque, and one by Visalberghi & Fragaszy (2002) using capuchin monkeys; both of them failed. There now appears to be general agreement among researchers that monkeys are not capable of imitating others (Visalberghi & Fragaszy, 1990, 2002; Galef, 1990; Whiten & Ham, 1992).

Finally, there is a lack of studies examining intentional or emotional attribution to others by monkeys – or at least, a lack of reported successful studies. Capuchin monkeys may provide reassurance to distressed individuals, but they fail to initiate consolation (initiate reassuring contact with a victim; Verbeek & de Waal, 1997). Reports from field studies are also notably quiet about empathic behaviours in monkey species. One possible explanation, of course, is that relevant behaviours have not been observed yet. However, given the wealth of observational data obtained over many decades, it is also possible that a lack of reports accurately reflects a lack of relevant behaviour.

1.8.3. Metarepresentations

Data on monkeys showing behaviours indicative of secondary representations are scarce, and there are even less data concerning behaviours indicative of metarepresentational abilities, which is perhaps not surprising given that metarepresentational abilities are based on secondary representational abilities (Perner, 1991). No studies to date have addressed false belief understanding or appearance-reality distinctions in monkeys. There is one study attempting to test for episodic memory in rhesus macaques, which failed to find any evidence for it (Hampton, Hampstead & Murray, 2005).

1.9. Purpose and scope of the present work

Looking at the available evidence for mental representational abilities (see Table 1.1), one might be tempted to conclude that there is no evidence for anything other than primary representational abilities in monkeys (Suddendorf, 1999). However, this conclusion might be premature, given that for some tasks suggestive of secondary representational abilities relevant data are simply not available for monkeys. Clearly, more data would help us to draw a more complete picture of primate representational abilities.

The present work aims to investigate secondary representational abilities in monkeys more closely in order to provide a more accurate and detailed account of monkeys' mental representational abilities. Such data could potentially reveal similarities and differences in cognitive abilities between monkeys and apes (both human and nonhuman), and potentially help in tracing the evolution of hominid cognitive abilities.

Table 1.1. General overview of evidence for representational abilities in children, apes and monkeys

		Children			Apes		Monkeys	
		Study	Age	Evidence?	Study	Evidence?	Study	Evidence?
Primary Representation	Neonatal imitation	Meltzoff & Moore, 1977	< 7 days	YES	Bard & Russell, 1999	YES	Ferrari et al., in prep	YES
	Visible displacement	Hofstadter & Reznick, 1996	8-12 months	YES	Poti & Spinozzi, 1994	YES	Dumas & Brunet, 1994	YES
Secondary Representation	Pretend play	Corrigan, 1987	1.5-2 years	YES	Hayes, 1951	YES	?[1]	?[1]
	Invisible displacement	Haake & Somerville, 1985	1.5 years	YES	Call, 2001	YES	De Blois & Novak, 1994	MIXED
	Means-ends reasoning	Bullock & Luetkenhaus, 1988	1.5-2 years	YES	Visalberghi et al., 1995	YES	Visalberghi & Limongelli, 1994	NO
	Understand external representations	DeLoache, 1991	2.5 years	YES	Kuhlmeier et al., 1999	YES	Fagot et al., 1999	MIXED
	Mirror self-recognition	Amsterdam, 1972	1.5-2 years	YES	Gallup, 1970	YES	Anderson, 1984	NO
	Attribute intentions and emotions	Zahn-Waxler et al., 1979	2 years	YES	Call & Tomasello, 1998	YES	?[1]	?[1]
	Generalised imitation	Asendorpf et al., 1996	1.5 years	YES	Hayes & Hayes, 1952	YES	Mitchell & Anderson, 1993	NO
	Imitation recognition	Meltzoff, 1990	14 months	YES	Nielsen et al., 2004	YES	?[1]	?[1]
Meta-representation	False belief	Wimmer & Perner, 1983	4.5 years	YES	Call & Tomasello, 1999	NO	?[1]	?[1]
	Appearance-reality distinction	Flavell et al., 1983	4 years	YES	?[1]	?[1]	?[1]	?[1]
	Episodic memory / source memory	Wimmer et al., 1988	4 years	YES	Menzel, 1999	YES	Hampton et al., 2004	NO
	Understand desire	Moore et al., 1995	5 years	YES	?[1]	?[1]	?[1]	?[1]

[1] = no reports or assessments of this ability are found in the literature

1.10. Justification of study species

Two species were tested in the course of the present work: pig-tailed macaques, *Macaca nemestrina*, and tufted capuchin monkeys, *Cebus apella*. Pig-tailed macaques represent an Old World monkey species, sharing a common ancestor with humans as recently as 20 million years ago (Tomasello & Call, 1997). Capuchin monkeys on the other hand are a New World monkey species, having separated from a common ancestor with humans ca. 35 million years ago (Tomasello & Call, 1997). A comparison of these two species is interesting in that similar abilities might hint at the presence of the trait in question within a common evolutionary ancestor, which subsequently may have been maintained in both species. Alternatively, similar abilities might have evolved independently in both species, perhaps due to similar ecological pressures. A short description of both species' natural ecology might help to outline potential differences.

1.10.1. *Macaca nemestrina* ecology

Macaca nemestrina, common name pig-tailed macaque, is part of the family Cercopithecidae, with 4 different recognised subspecies (Rowe, 1996). Pig-tailed macaques are native to south-east Asia ranging from Burma to the Malay Peninsula and Sumatra (Rowe, 1996). These monkeys live in multimale-multifemale groups of 15-40 individuals with 1 male to 5-8 females and a home range of 5-15 square kilometres; females have a matrilineal dominance hierarchy, and males emigrate from their native groups (Caldecott, 1986). Pig-tailed macaques are diurnal, arboreal and terrestrial, spending most of their time in the lower to middle canopy (Caldecott, 1986). Their diet mostly consists of fruit and seeds, but also animal prey and leaves (Rowe, 1996). Infants are weaned at ca. 12 months, females reach sexual maturity at ca. 35 months, and may give birth every 12-24 months; their life expectancy in the wild is ca. 26.3 years (Rowe, 1996).

Pig-tailed macaques have a unique facial expression called the "pucker", whose meaning as a social signal is disputed; however, it has been interpreted as an affiliative gesture with a general distance-reducing or summoning function (Maestripieri, 1996).

1.10.2. *Cebus apella* ecology

Cebus apella, common name tufted or brown capuchin monkey, is part of the family Cebidae, and comprises 6 or more different subspecies (Fragaszy et al., 2004). These monkeys are found in northern Central America, living in multimale-multifemale groups of 12-27 individuals (1 male to 3 females) with a home range of 0.25-3 square kilometres (Fragaszy et al., 2004). All groups have alpha males and females, however the dominance hierarchy below the alpha animals is somewhat fluid; males usually disperse from their native groups (Fragaszy et al., 2004). Capuchin monkeys are diurnal and arboreal, and largely feed on fruit, but also seeds and animal prey (Rowe, 1996). Capuchin monkeys are weaned at ca. 6 months, females reach sexual maturity at ca. 84 months, and give birth about every 22 months; their average life span is estimated to be around 40 years (Rowe, 1996), but individuals are known to have lived for over 50 years in captivity (Fragaszy et al., 2004). One peculiar behaviour of capuchin monkeys is urine washing, consisting of urinating onto the palm of the hands, the soles of the feet and the top of the tail, and often scratching the body afterwards. This behaviour appears to have multiple functions related to hygiene, thermoregulation and ectoparasites (Fragaszy et al., 2004). Capuchin monkeys have relatively large brains compared to their body size (Gibson, 1986), and are noted for their impressive tool use abilities (Beck, 1980; Fragaszy et al., 2004). Both these traits may be related to reliance on difficult-to-obtain food items (de Moura & Lee, 2004). Capuchin monkeys are also unusually tolerant towards familiar conspecifics (Fragaszy et al., 2004), making them a preferred subjects in many social and cognitive comparative studies.

It is evident that pig-tailed macaques and capuchin monkeys share some important ecological features. For example, both species live in multi-male multi-female groups, into which adult males may immigrate. Thus, if social pressures have influenced representational abilities, both species should show similar levels of mental complexity. However, differences are apparent in feeding ecology, as capuchin monkeys appear to feed more on difficult-to-obtain food items, which may require more advanced representational abilities. As discussed above, representational abilities also may convey general advantages in the areas of self-control or future planning, which might be expected to hold true for both species. On the other hand, a complete absence of secondary representational abilities in both species would suggest that advanced representational abilities evolved after the phylogenetic separation between monkeys and apes, and thereafter continued to refine in humans.

1.11. Representational complexity beyond comparative cognitive research

Although the present work focuses exclusively on evolutionary arguments for the phylogenetic origin of secondary representations in primates, it should be noted that cognitive complexity is also an important issue in the context of captive animal welfare. Cognitively complex abilities in themselves should not be relevant to welfare issues (Dawkins, 2001). Rather, it is the ability to suffer that should feed into welfare considerations (Mendl & Paul, 2004). Representational complexity cannot inform us about an individual's potential to experience pain, but if the assumption is made that animals have this potential, cognitive complexity can clarify under what circumstances suffering might occur (Bradshaw, 1998). For example, animals capable of representing highly aversive past events through the use of secondary representations may be more likely to suffer than animals that do not have secondary representations. On the other hand, secondary representational abilities might also reduce suffering if, for example, animals can anticipate that an aversive husbandry procedure is of limited duration rather than open-ended (Mendl & Paul, 2004). Suffering may be elevated in animals who have empathic reactions to suffering conspecifics, or who can attribute harmful intentionality to human caretakers. Increasing our knowledge of animals' representational abilities can therefore help in devising ways of minimising psychological stress and improving the welfare of captive animals.

1.12. Outline of presented work and justification of experimental tasks

In the following, pig-tailed macaques and capuchin monkeys were tested on several tasks aimed at revealing secondary representational abilities. Most of the work is situated within the context of the large body of data already available in the areas of imitation, mirror self-recognition and means-end reasoning. New aspects of secondary representations such as imitation recognition and even episodic memory as a metarepresentational achievement are also discussed. Chapter 2 examines self-imitation in pig-tailed macaques, aiming to reveal the extent to which macaques understand imitation as an abstract concept, and how the developed paradigm might be useful for episodic memory assessments. Chapter 3 looks at imitation recognition in both pig-tailed macaques and capuchin monkeys, attempting to discover if monkeys recognise intentionality in an imitator. The results of Chapter 3 gave reason to conduct a mark test on the same pig-tailed macaques, which is reported in Chapter 4. Chapter 5 describes a mirror study in capuchin monkeys, addressing a potential confound in the experimental procedure of mirror-exposure studies. Chapter 6 presents an experiment on means-end reasoning in capuchin monkeys outside of tool-using contexts. Finally, Chapter 7 summarises the obtained results and attempts to draw conclusions with regard to both pig-tailed macaques and capuchin monkeys' representational abilities.

Chapter 2: Self-Imitation in Pig-Tailed Macaques

This first data chapter examines imitative abilities in pig-tailed macaques. However, unlike most previous work which studied monkeys' ability to imitate a human model, the present study assessed if monkeys are capable of imitating (repeating) their own previously performed actions. This chapter defines 'imitation' for the present context, and outlines to what extent imitative abilities can be based on secondary representations. An experiment using a 'self-imitation' paradigm is then reported, and it is discussed if the monkeys' performance can be considered to be based on secondary representations. In addition, the paradigm's relations to 'other-imitation' paradigms and episodic memory abilities are evaluated.

2.1. Definition of imitation

Imitation forms a subclass of social learning processes, which have most comprehensively been summarised and defined by Zentall (1996). Social learning is obviously a social phenomenon, which broadly defined involves the alteration of individual A's behaviour through the presence or influence of, or direct manipulation by, individual B (Zentall, 1996). However, not all behaviours that follow this pattern can be classed as social learning (e.g. agonistic encounters); rather, all instances of social learning involve these elements. Several subclasses of social learning processes have been proposed, listed in the following ascending order of cognitive complexity. At its most primitive, *contagion* refers to an increase in behaviours that form part of an individual's natural behavioural repertoire which can be socially induced, such as synchronized courtship displays. *Social facilitation*, also called *social enhancement*, are behaviours influenced by the mere presence of a conspecific, e.g. the induction of eating behaviours through the presence of other individuals. *Local enhancement* involves an individual having its attention drawn to a particular place due to the presence of a conspecific in that place. Similarly, *stimulus enhancement* draws the attention of an individual to a particular object due to another animal interacting with this object. An individual engaging in *goal emulation* attempts to reproduce the outcome of a model's action rather than an accurate replication of the model's actions. Finally, the term *(true) imitation* has been reserved for actions that are "copying (an) act or utterance, or some act for which there is clearly no instinctive tendency" (Zentall, 1996, pp. 231).

Several variations of the definition of imitation can be found in the literature. For example, Visalberghi & Fragaszy (2002) defined an act A as imitation when act A is similar to an observed act B, B has to be observed prior to the production of A, A is intended to be similar to B, and A constitutes a behaviour not already present in the organism's repertoire. However, knowing which behaviours have or have not been previously been performed by an individual may in many cases be impossible to assess. An alternative version, which Visalberghi & Fragaszy (2002) called 'imitation *sensu* Meltzoff', applies the same criteria as Visalberghi and Fragaszy's first definition with the only difference that it allows for imitation to occur for contexts in which the imitation behaviour is known to be already part of the animal's behavioural repertoire. Imitation for the current context will be defined following Herman (2002), in which imitation is defined as "the process of accessing a mental representation of an experienced event to reproduce that event through one's own behaviour" (pp.66).

2.2. Imitation and representational complexity

Although Perner (1991) himself did not list imitation as an ability based on secondary representations, others have. Whiten (1996) compared imitation to pretence, which according to Perner (1991) is one of the first indicators of secondary representational abilities in human infants (see also Jarrold et al., 1994). Pretence is only possible if multiple mental models can be conceived and co-ordinated, such as "this is a banana" (primary representation) whilst at the same time pretending that "this is a telephone" (secondary representation; Leslie, 1987). According to Perner (1991), confusion between primary representations of the object (banana) and secondary representations of the pretended situation ("this is a telephone") can be avoided by tagging secondary representations with 'suppose' attitudes, which can be held in parallel to primary representations. This solution to the representational confusion of what a given object really is and what it is merely pretended to be allows for pretence abilities based on secondary representations alone and in the absence of metarepresentational abilities.

Whiten (1996) argued that imitation can be viewed as a particular form of pretence. For example, when seeing individual A performing behaviour X, imitation of behaviour X could be achieved by *pretending* to be individual A performing behaviour X. In other words, all one needs to do to imitate individual A is to act *as if* one were individual A. Cognitively, imitation seen as a form of pretence implies that an imitator can hold an explicit mental representation of the model's behaviour in mind (secondary representation) whilst attempting to match his own behaviour and circumstances (primary representation) to the secondary representation. This is not to say that all instances of imitation are achieved through processes involving secondary representations. Imitation may also be based on primary representations, e.g. in the case of neonatal imitation (Meltzoff & Moore, 1977), infants match the visual input from a model to their own kinaesthetic motor outputs. Secondary representations are not required in this case, because a single updating representation of the model's actions is sufficient to achieve imitation without the need to represent the model's actions as 'detached' from the immediate environment. Hence, in order to infer secondary representations from imitative contexts, one would need to show that the model's actions are (i) explicitly represented, (ii) can be drawn upon in the absence of the model, and (iii) can be replicated even when other input was received from the model in-between the act of witnessing and executing the imitative act (hence showing a detached representation). For the current discussion, imitation in the context of replicating motor movements but not involving objects will be considered.

2.3. Imitation in human infants

Several decades of research into the imitative abilities of humans and nonhumans have provided quite a detailed picture of who can imitate, what types of actions can be imitated, at what age, and under what circumstances. Imitation (*sensu* Meltzoff) of motor movements occurs at a very young age in humans. After seeing an experimenter's facial gesture (such as mouth opening, lip protrusion, tongue protrusion), neonates (<24h) will respond with the same facial gesture (Meltzoff & Moore, 1977; Meltzoff & Gopnik, 1994). However, as argued above, neonatal imitation is not based on secondary representations, since infants can achieve neonatal imitation by matching the visual input of the model's action with their own kinaesthetic perceptions, which in turn can be achieved through the use of primary representations alone (Perner, 1991).

True imitation can be found in infants in the form of pretend play as early as 18 months (Berk, 2000). For example, if an infant is pretending to drink from an empty cup, it can be thought of as e.g. imitating her mother drinking from a cup. As this type of pretend play occurs in the absence of a live model (i.e. without the mother actually drinking from a cup being present), and supposedly the last action the infant saw the mother perform was an action different to drinking from a cup, the infant can be thought of as retrieving a detached representation of her mother drinking from a cup. As such, the child needs to utilise secondary representations for successful deferred imitation, which enable it to conceive of the earlier action (secondary representation) in its perceptual absence.

2.4. Imitation in apes

One might expect to find similar imitative abilities in great apes and humans, and indeed this appears to be the case. For example, Hayes & Hayes (1952) conducted an experimental study testing for a generalised understanding of imitation in the home-reared chimpanzee Vicki. Vicki was presented with 70 actions, some involving objects, and was encouraged to repeat these actions after the command "Do this!". If the correct action was repeated by Vicki, she received a food reward. Hayes & Hayes (1952) report that at first, Vicki had to be put through actions several times before being able to repeat them, but after learning to respond to 11 such actions, Vicki was able to repeat many actions spontaneously with the first attempt. This level of imitation, however, does not necessarily rely on secondary representational abilities, since (as in the case of neonatal imitation) a single updating model of reality is sufficient to match self-performed actions with the model's action. In order to infer secondary representations, one would need to show that Vicki could perform these actions whilst observing the model engaging in other activities before attempting to replicate the target actions. Anecdotally, Vicki appeared capable of this level of imitation. Vicki is reported to have imitated several actions she had observed in her caregivers, such as dusting the furniture, washing the dishes, or applying lipstick with the use of a mirror (supposedly without having witnessed these actions just prior to the imitative acts).

Custance, Whiten & Bard (1995) replicated Hayes & Hayes' (1952) original approach with two chimpanzees (also Custance & Bard, 1994). These chimpanzees were first trained (using food rewards) to imitate 15 arbitrary actions (e.g. raise foot, touch chin etc.), none of which involved objects. The crucial testing phase consisted of 48 novel arbitrary actions being presented to the chimpanzees, and spontaneous imitation of these new, untrained actions was evaluated. Custance and colleagues found that observers recognised the imitated actions significantly above chance levels, and concluded that chimpanzees, after a period of training, are capable of bodily imitation. Similar results were subsequently reported for a language-trained orang-utan (Miles et al., 1996). There are also recent reports on deferred imitation involving deferred object-related actions in chimpanzees and orang-utans (e.g. Bering, Bjorklund & Ragan, 2000; Bjorklund, Yunger, Bering & Ragan, 2002; Bjorklund, Bering & Ragan, 2000; but see also Yunger & Bjorklund, 2004, for failure to replicate some of the earlier findings).

2.5. Imitation in monkeys

A few attempts have been made to teach monkeys to imitate bodily actions, without success. Mitchell & Anderson (1993) were able to condition scratching behaviours in a pig-tailed macaque so that the macaque was scratching himself whenever an experimenter was scratching. However, the macaque did not scratch the body part corresponding to the body part the experimenter was scratching. Visalberghi & Fragaszy (2002) also report several imitation tests of either object-directed or self-directed actions in capuchin monkeys, some using "Do this!" commands. None of the capuchins showed any reliable imitative abilities, although self-directed actions were judged to be less accurate than object-directed actions. Researchers now largely agree that monkeys are simply not capable of imitating at this level (Visalberghi & Fragaszy, 1990, 2002; Galef, 1990; Whiten & Ham, 1992; but see also Voelkl & Huber, 2000, for claims of imitation in marmosets).

2.6. Imitation in other animals

A few species of non-primates have also been reported capable of imitating bodily actions. For example, a parrot tested by Moore (1996) repeated 7 arbitrary actions as demonstrated by a human experimenter, such as waving an arm (wing) and saying 'Ciao'. Bottlenosed dolphins matched 8 out of 12 of a human model's arbitrary bodily actions, such as spinning on the spot or waving an arm (flipper; Herman, Pack & Morrel-Samuels, 1993; Herman, 2002). An anecdotal report also exists for the imitation of a fur seal by a dolphin (Tayler & Saayman, 1973). These examples are particularly remarkable in that the model's body and actions were structurally and perceptually very different from the animals' bodies, yet transfer of the actions to their own "corresponding" body parts occurred. However, these generalised concepts of imitation nonetheless may indicate no more than primary representational abilities.

2.7. Self-imitation in bottlenosed dolphins

Bottlenosed dolphins have been the subject of the only 'self-imitation' study ever conducted with nonhumans. Rather than repeating a model's most recently performed behaviour, two bottlenosed dolphins were trained to repeat their own most recently performed behaviour using an abstract 'repeat' gesture as a signal. Both dolphins successfully generalized the repeat rule to four novel, untrained behaviours (Mercado, Murray, Uyeyama, Pack & Herman, 1998; Herman, 2002; see also Mercado, Uyeyama, Pack & Herman, 1999, for repetition of object-directed actions).

Although these achievements do not strictly fall under the definition of imitation (because the dolphins were replicating their own actions, not those of another individual), this paradigm seems nonetheless to inform us about the animals' representational abilities. Since repeat performances of behaviours were established through positive reinforcement techniques, it is conceivable that a performed behaviour was stored as a primary representation that guided the subsequent repetition performance. Secondary representations were not required at this point, since simple kinaesthetic-kinaesthetic matching behaviours may have been sufficient to facilitate successful repeat performances. In relation to "Do this!" studies, if "Do this!" is more accurately viewed as a "Do-what-I-did" command, self-imitation paradigms can perhaps more accurately be described as involving a

"Do-what-you-did" command. Both paradigms aim to assess the flexibility and generalisability of imitative abilities.

2.8. Self-imitation in monkeys

The remainder of this chapter reports the first attempt to test self-imitation abilities in a monkey species. Building upon Mercado et al. (1998), pig-tailed macaques were trained to perform three distinct self-directed behaviours in response to auditory cues, and subsequently to repeat two of the behaviours after hearing a neutral 'repeat' command. The monkeys were then tested with regards to the nature of the representation used for successful repetition, i.e. whether the auditory signal or the repetition performance itself facilitated repetition, and if transfer of the repeat signal to novel, untrained behaviours occurred. Both these types of tests are aimed at validating that the monkeys relied on primary representations for successful task performance.

In order to infer secondary representations, it was aimed to show that monkeys could repeat a target action even if other actions were performed in between the target action and the repeat command. To fulfil this requirement, n-back trials were planned to be conducted. N-back trials involve the performance of a target behaviour paired with a signal to 'tag' the behaviour as the target behaviour. Further behaviours would then be performed before the animal is asked to repeat the previously tagged target behaviour. This arrangement means that the animal cannot rely on primary representations of the most recent performed target behaviour, but has to access a secondary representation of the target behaviour for successful repetition performance. N-back trials are readily used in tests with human participants, however to date this technique has not been employed with nonhumans, and it remains to be seen whether any species other than humans can perform such tasks successfully.

2.9. General methods and basic training

2.9.1. Subjects and housing

The subjects were four male pig-tailed macaques (*Macaca nemestrina*), Alcatraz (18 years), Papa (15 years), David (5 years) and Charlie (4 years), all captive-born and housed at the Dipartimento di Neuroscienze, Universita di Parma. Although the monkeys were housed individually, their home cages (cage measures: 100x160x100cm) were part of an interconnected system that allowed daily social interactions with other individuals. The monkeys were not food deprived for the experiment, but received part of their normal diet during testing and the rest thereafter. Water was available ad libitum. Although training started with all four monkeys, Papa and David failed to learn the basic repeat signal even after 8 months of almost daily training. Therefore, only Alcatraz's and Charlie's results are reported and discussed. Details of Papa's and David's training can be found in the Appendix.

2.9.2. Procedure

All monkeys were individually trained and tested in their home cages. Two training sessions were administered on a daily basis, one in the morning and one in the afternoon. Each session lasted between 15 and 30 minutes depending on the number of trials administered, but never exceeded 30 minutes continuous training. The experimenter sat in front of the cage with the apparatus for producing auditory stimuli and a clipboard for recording the monkeys' responses. A white cardboard screen (ca. 40x70cm) covered the apparatus to avoid visual cueing of the target behaviour. The food rewards (small pieces of apple, pear, carrot, banana, orange, fennel, pumpkin seeds, raisins, and peanuts) were placed on a tray next to the experimenter. Whenever a monkey performed a desired response, a metallic clicking noise was sounded as a secondary reinforcer (Clicker, Canac) before a food reward was given.

The first step in training the monkeys to repeat self-directed behaviours on signal was to increase the spontaneous occurrences of these behaviours. The second training phase consisted of bringing these behaviours under signal control, i.e. training the monkeys to associate a distinct auditory signal with each behaviour. In the third training phase, the monkeys were taught to repeat two of these behaviours after hearing a novel 'repeat' signal.

2.9.3. Training 1: Establishing three self-directed responses

Three distinct self-directed behaviours were selected for training. Scratching and grooming are both trainable through operant conditioning techniques (e.g. Louboungou & Anderson, 1987; Iversen, Ragnarsdottir & Randrup, 1984; Anderson, Fritsch & Favre, 1990), and therefore were considered suitable for this experiment. Mouthing of one hand was chosen as the third behaviour on the basis that mouthing forms part of the monkeys' natural behavioural repertoire. This first training phase consisted of increasing these behaviours' frequencies through positive reinforcement training.

2.9.3.1. Scratching

A scratch was defined as two or more movements of the fingertips drawn rapidly across the skin in quick succession at the same body area. Training started with eight 30-minute sessions of baseline measures of scratching behaviours. During the first four baseline sessions, no rewards were given and any occurrences of scratching were noted. During the next four baseline sessions, 30 rewards were given to the monkey at one minute intervals independent of the monkey's behaviour, and all occurrences of scratching were noted. During each training session thereafter, all occurrences of scratching were rewarded. One monkey (Charlie) was initially trained for both scratching and grooming (see below); however, after several training sessions his grooming and scratching responses became largely indistinguishable. In order to differentiate between scratching and grooming responses, scratching with the foot directed to the shoulder was considered the only acceptable scratching response for Charlie.

2.9.3.2. Grooming

Grooming was defined as a self-directed manual response accompanied by intense visual interest in the body part being groomed, e.g. manipulating hairs or skin and removing single hairs or particles from it. At least two such grooming movements had to occur in order to be counted as a grooming response. Six baseline measurements of grooming were taken during the training of signal control for scratching, i.e. when rewards were given after scratching behaviours in response to the scratch signal. All sessions after baseline sessions involved reinforcement of every grooming response.

2.9.3.3. Mouthing

Mouthing was defined as licking a hand or wrist, or inserting a hand or wrist into the mouth. Baseline measures of mouthing were collected during six training sessions of signal control for scratching and grooming, i.e. when rewards were available contingent on scratching and grooming responses after the respective scratch and groom signal had been sounded. Since mouthing responses never occurred spontaneously during baseline, a small number of additional training sessions were interspersed with normal training sessions, in which the experimenter applied some fruit juice onto the monkeys' wrists and hands with a syringe. Every lick of the hand was then additionally reinforced with a food reward. Monkeys were rewarded for all occurrences of mouthing during normal training sessions, which took place once the monkeys' wrists had completely dried.

2.9.3.4. Results

Figure 2.1 shows the number of scratching responses during baseline and training. It is evident that contingent reinforcement had a dramatic effect, increasing scratching responses from fewer than 10 occurrences during baseline to up to almost 140 occurrences during contingent reinforcement. Similar effects were obtained for grooming (Figure 2.2) and mouthing (Figure 2.3), although these behaviours were less frequent than scratching.

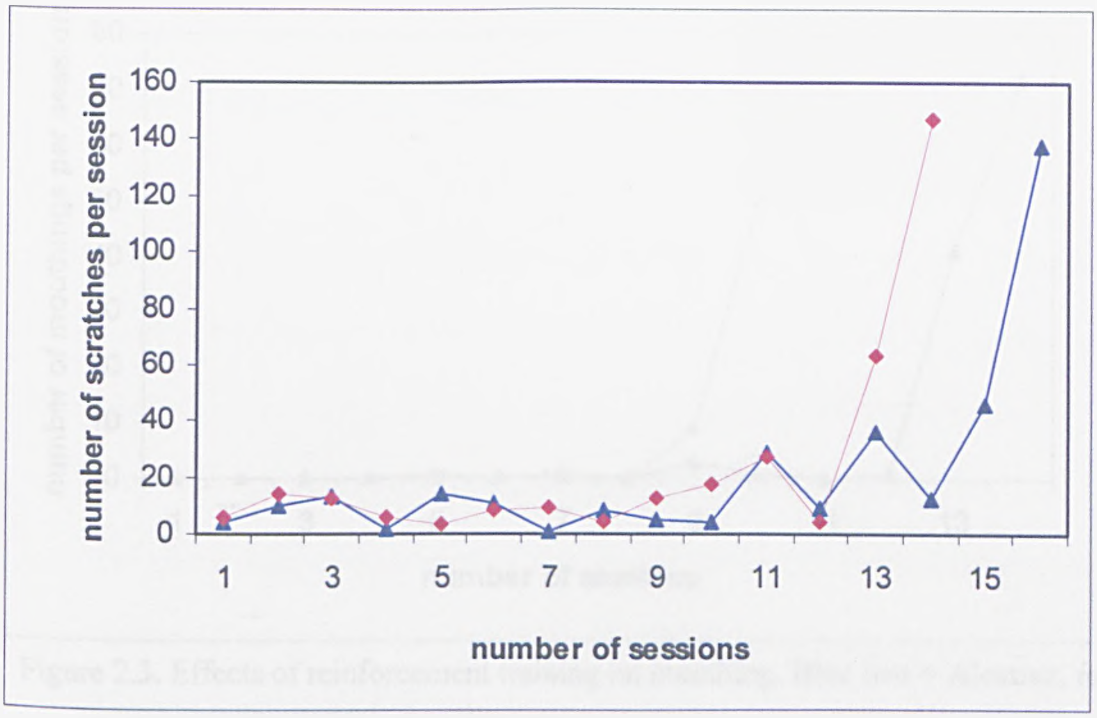

Figure 2.1. Effects of reinforcement training on scratching. Blue line = Alcatraz, red line = Charlie. First 8 sessions = baseline.

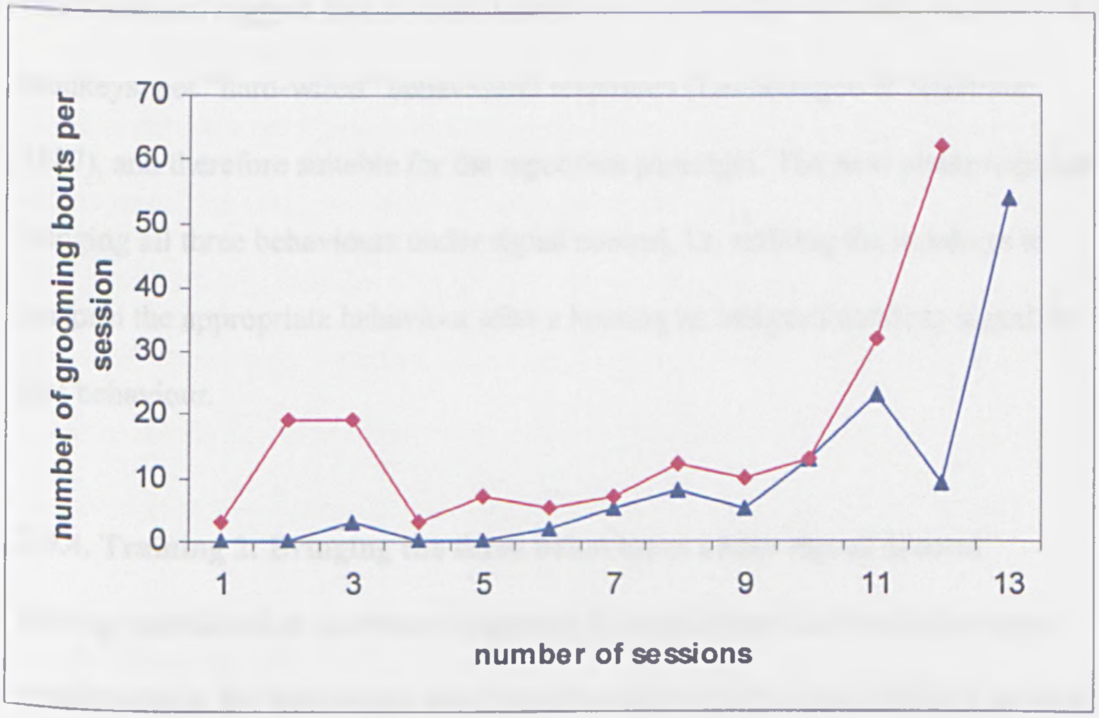

Figure 2.2. Effects of reinforcement training on grooming. Blue line = Alcatraz, red line = Charlie. First 6 sessions = baseline.

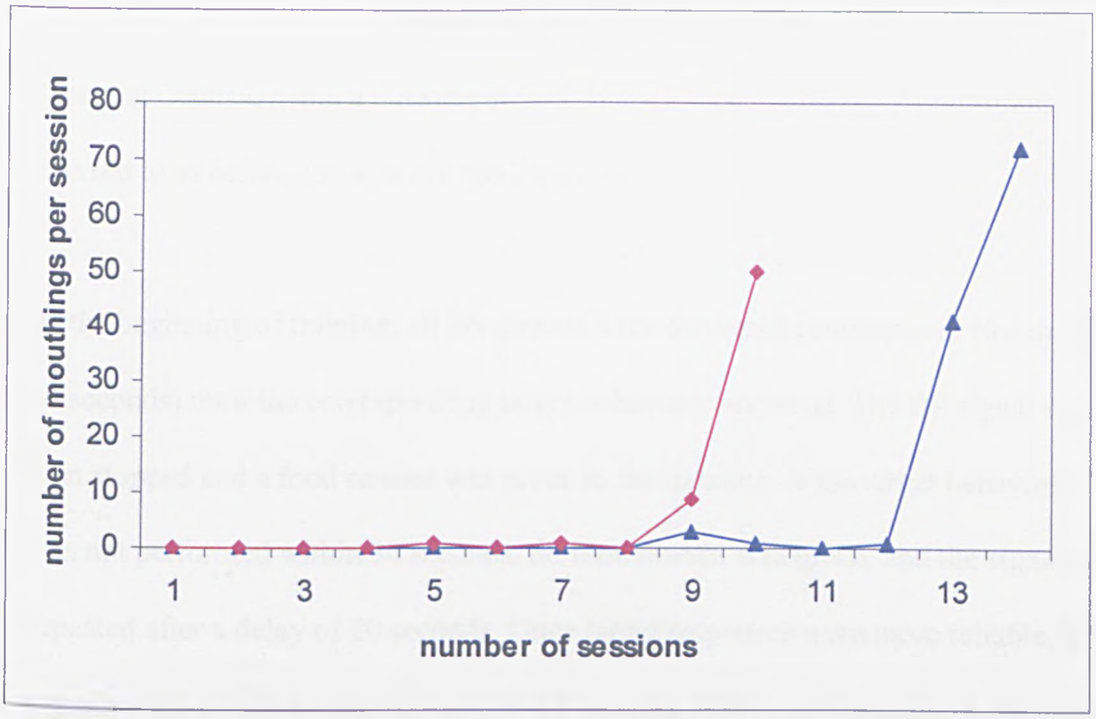

Figure 2.3. Effects of reinforcement training on mouthing. Blue line = Alcatraz, red line = Charlie. First 6 sessions = baseline.

Dramatic increases in performance after introduction of continuous contingent reinforcement suggest that all three behaviours were under voluntary control of the monkeys, not "hard-wired" behavioural responses (Louboungou & Anderson, 1987), and therefore suitable for the repetition paradigm. The next phase required bringing all three behaviours under signal control, i.e. training the monkeys to perform the appropriate behaviour after a hearing an assigned auditory signal for that behaviour.

2.9.4. Training 2: Bringing the three behaviours under signal control

Having established an increased frequency for each behaviour contingent upon reinforcement, the behaviours were brought under signal control (defined as each behaviour occurring reliably after the appropriate signal had been given). Three distinct auditory sounds were used as signals: one high-pitched sound and one low-pitched sound, both generated with an electronic keyboard ("Fun Keyboard", Early

Learning Centre©), and a clicking noise ("Baby Phone", chicco). These sounds are referred to as behaviour-specific (BS) signals.

At the beginning of training, all BS signals were delivered continuously (for up to 30 seconds) until the corresponding target behaviour occurred. The BS signal was then stopped and a food reward was given to the monkey. If the target behaviour was not performed within 30 seconds, no food reward was given, and the signal was repeated after a delay of 20 seconds. Once target responses were more reliable, BS signals were sounded continuously for 10 seconds. If the corresponding behaviour occurred within this period, the BS signal stopped and a reward was given. If no observable behaviour or an inappropriate behaviour occurred, trials were ended after the 10 second BS signal, no reward was given and the trial was scored as "no response" or "wrong response" respectively. Inter-trial intervals were set at 20 seconds. Thirty trials for each behaviour were administered during each session. Both monkeys were trained on scratching and grooming responses first, and training of the mouthing response was only introduced after scores of at least 80% were achieved correctly for both scratching and grooming behaviours in two consecutive sessions. Behaviours were first trained in alternating blocks of 10 trials, then blocks of five, and finally in random order. A score of at least 80% correct for all three behaviours in two consecutive sessions was taken to indicate signal control.

2.9.4.1. Results

Figure 2.4 and 2.5 show Alcatraz's and Charlie's respective performances summarized as the average percentage of correct trials over 120 trials (four sessions). More trials were required to learn the scratch and groom responses than for mouthing, suggesting that the initial training on scratching and grooming might have facilitated generalization of signal control to mouthing responses. Figures 2.4 and 2.5 also show that both monkeys' grooming responses decreased upon introduction of the mouthing response trials, but recovered quickly to criterion performance. It is possible that the monkeys initially confused grooming and mouthing responses, as both these actions (but not scratching) were used during natural grooming bouts (personal observations).

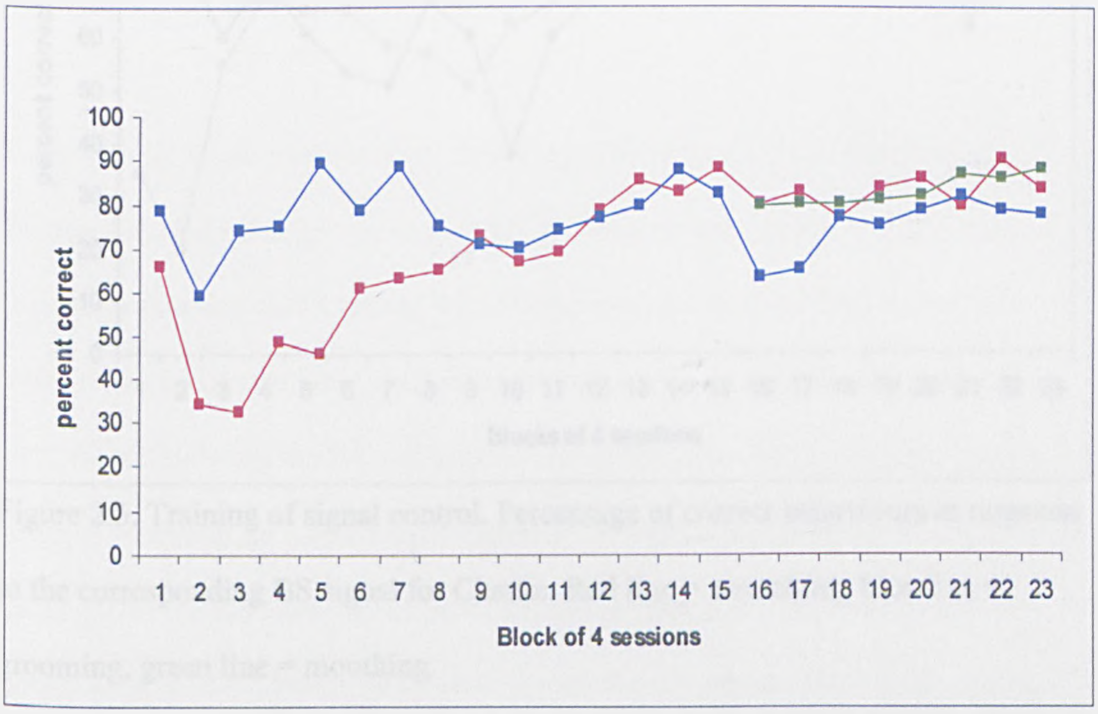

Figure 2.4. Training of signal control. Percentage of correct behaviours in response to the corresponding BS signal for Alcatraz. Red line = scratching, blue line = grooming, green line = mouthing.

After an average of 117 sessions, the monkeys had learned to respond to all three BS signals with appropriate self-directed behaviours (over 80% correct in two consecutive sessions). Having achieved signal control for all three behaviours, the final training phase introduced the repeat signal for two of the trained behaviours.

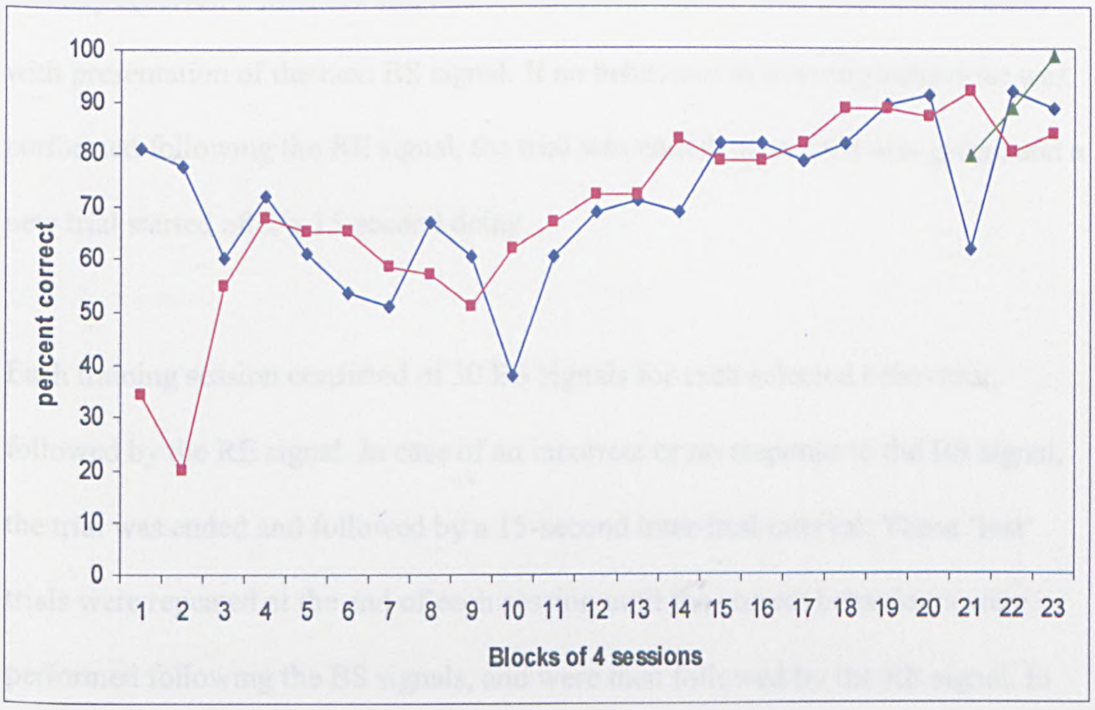

Figure 2.5. Training of signal control. Percentage of correct behaviours in response to the corresponding BS signal for Charlie. Red line = scratching, blue line = grooming, green line = mouthing.

2.9.5. Training 3: Repetition of two behaviours following a repeat signal

Once the monkeys responded reliably to all three BS signals, two behaviours were selected for each monkey (Alcatraz: scratch and groom; Charlie: scratch and mouth) for training of repetition following a neutral 'repeat' (RE) signal. A small metal whistle was blown to give the RE signal (the whistle remained in the experimenter's mouth throughout training sessions and therefore did not provide visual cues).

Each trial consisted of a BS signal (max. 10 seconds), which stopped as soon as the monkey performed the appropriate behaviour, followed by a food reward being given to the monkey. After a 3-second delay, the RE signal was given for up to 10 seconds. If the monkey repeated the previous behaviour, the signal stopped, the monkey received a food reward, and the next trial started after a 10-second delay with presentation of the next BS signal. If no behaviour or a wrong behaviour was performed following the RE signal, the trial was ended, no reward was given, and a new trial started after a 15-second delay.

Each training session consisted of 30 BS signals for each selected behaviour, followed by the RE signal. In case of an incorrect or no response to the BS signal, the trial was ended and followed by a 15-second inter-trial interval. These 'lost' trials were repeated at the end of each session until the correct behaviours were performed following the BS signals, and were then followed by the RE signal. In order to maintain the learned third response, 20 signals for the third behaviour were given (10 at the start and end of each session; performance remained consistent above 80% correct), but never combined with the RE signal. BS signals were first presented in homogenous blocks of five and then, once the monkey were responding reliably (more than 80% correct in two consecutive sessions), in random order. Monkeys were judged to have learnt the RE signal if they performed both repeat behaviours at over 80% correct in two consecutive sessions of randomly ordered signals.

After reaching this criterion, the monkeys received further formal cued repetition sessions to ensure that the behaviours were repeated only after the RE signal and not otherwise. For Alcatraz, each session consisted of 20 trials of the scratch signal followed by the RE signal, and 20 trials of the groom signal followed by the RE signal (Charlie: scratch and mouth). In addition, the monkeys received a further 20 trials of each behaviour not combined with the RE signal, but followed by a 10-second observation period and any instances of the target behaviour were noted. Trials for each behaviour were administered in random order, and were separated by 10-second inter-trial intervals.

2.9.5.1. Results

Figures 2.6 and 2.7 show Alcatraz's and Charlie's learning curves for the RE signal. While Alcatraz's repeat responses (Figure 2.6) were quite accurate from the start of training (averaging around 70%), Charlie's responses (Figure 2.7) were initially random, but improved slowly as training progressed. Alcatraz required 55 sessions and Charlie 113 sessions to reach criterion.

During the formal cued repetition phase, both monkeys showed erratic drops in their repeat performances throughout training. Alcatraz displayed a strong tendency to repeat target behaviours even in the absence of the RE signal, whereas Charlie never repeated behaviours without the RE signal. Charlie's mouthing performance diminished following the introduction of non-repeat trials, but slowly recovered to criterion. No such effect was observed for Alcatraz. Alcatraz required 32 sessions and Charlie 16 sessions to learn the basic task, i.e. to respond appropriately to auditory signals with three self-directed behaviours, and to repeat those two behaviours if and only if a RE signal was sounded.

Figure 2.6. Training to the RE signal. Percentage of correct repetitions in response to the RE signal for Alcatraz. Blue line = scratching, red line = grooming.

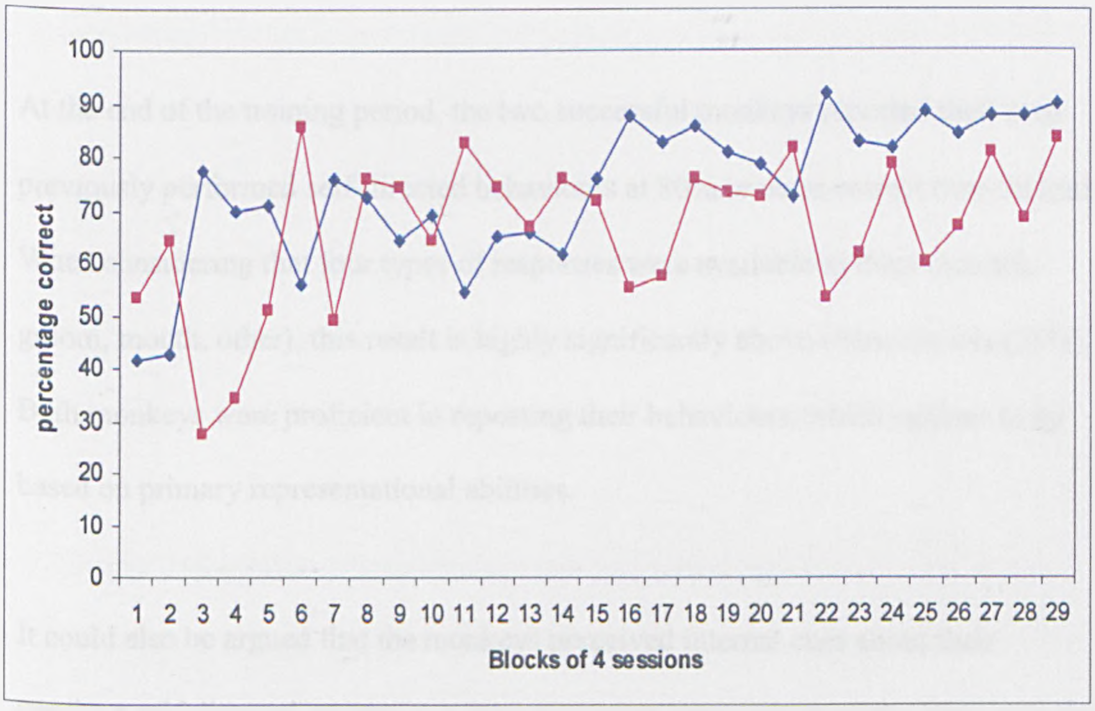

Figure 2.7. Training to the RE signal. Percentage of correct repetitions in response to the RE signal for Charlie. Blue line = scratching, red line = mouthing.

2.9.6. Discussion

Two pig-tailed macaques were trained to perform distinct self-directed behaviours in response to specific auditory signals, and to repeat two behaviours after hearing a neutral repeat signal. Two further macaques learned to perform three distinct self-directed behaviours in response to auditory signals, but failed to correctly repeat two behaviours after a repeat signal (for details, see Appendix). There are no obvious reasons why the two unsuccessful macaques failed to respond correctly to the repeat signal. All four monkeys were treated in the same manner, and received equal numbers of training sessions. One possibility is that there are individual differences in other cognitive abilities, which may support repetition performance. Motivational differences may also account for the observed individual variability, although all monkeys always accepted the food rewards.

At the end of the training period, the two successful monkeys repeated their own previously performed self-directed behaviours at 80% or more correct over 30 trials. When considering that four types of responses were available to them (scratch, groom, mouth, other), this result is highly significantly above chance levels (25%). Both monkeys were proficient in repeating their behaviours, which appears to be based on primary representational abilities.

It could also be argued that the monkeys perceived internal cues about their previous self-directed actions, e.g. somatosensory after-effects on the body area that was scratched, which could have prompted correct repetition performance. However, it could be expected that internal cues are more salient at the start of a session, and that habituation effects would make somatosensory feedback an unreliable indicator for the target behaviour after several target responses. On informal inspection, repeat performances at the beginning of a session did not appear to be significantly better than repeat performances at the end of a session, which supports the view that internal cues did not influence repetition performance.

Having argued that repetition performance is likely to be based on explicit representations, the first experimental test was conducted to validate this assumption. If the monkeys hold primary representations of the target episode, it is conceivable that the target episode might be represented in detail, and temporally extended to what occurred before and after the monkeys' actions. For the present purpose, the target episode is defined as starting with the first BS signal and including all aspects up to and including the RE signal. As such, the target episodes actually consist of an indeterminate number of elements that might be remembered; e.g., position in cage (where), experimenter involved (who), type of food reward received (what), and so on. Primary representations of the target episode should enable the monkeys to recall multiple independent aspects of this episode. In the following tests, the mnemonic salience of two elements within the target episode was assessed: the BS signal and the corresponding motor output.

2.10. Test for multiple memory elements of a target episode

Repetition performance could be based on representations of the motor behaviour without recollection of the initial BS signal; memory of the BS signal without recollection of the motor behaviour; or memory of both aspects combined into an integrated trace. Primary representations of the target episodes should allow the monkeys to recall these aspects independently of each other. In order to assess which elements are actually represented by the monkeys, three separate tests were conducted. Test 2.1 assessed whether the monkeys would perform the target behaviour in response to the RE signal when the initial target behaviour was performed spontaneously, in the absence of the BS signal. Test 2.2 elaborated on the initial test by giving the RE signal twice, thus requiring the monkeys to repeat target behaviours a second time without cueing through a BS signal. In both tests, the monkeys needed to remember their recent motor behaviour, rather than the BS signal. Test 2.3 tested if the monkeys could repeat the appropriate behaviour even when they did not perform the target behaviour but only heard the BS signal, meaning that the monkeys had to remember the BS signal for successful repetition. For the purpose of comparison, chance levels of correct test performance were defined as 25% correct repetition performance for all three tests, on the basis that the monkeys had four distinct responses categories available to them (scratch, groom, mouth, none of the above). It was hypothesised that repetition of the target behaviour significantly above chance levels on all three tests would be an indicator of explicit, primary representations.

2.10.1. Test 2.1.

Over three sessions, a total of 60 trials were given: 30 scratch signals and 30 groom signals in random order, each followed by the RE signal (Charlie: scratch and mouth). In addition, 30 episodes of each spontaneously performed target behaviour were rewarded and, after a 3-second delay, were followed by the RE signal. If the rewarded target behaviour was performed after the RE signal, another food reward was given to the monkey. Trials were separated by 20-second inter-trial intervals. Successful repetition of spontaneous behaviours could not be based on memory of the BS signal (because none was given), but had to be based solely on the memory of enacting the behaviour itself.

2.10.2. Test 2.2.

Sixty trials consisting of the scratch signal followed by the RE signal and 60 trials consisting of the groom signal followed by the RE signal were administered in random order over three sessions (Charlie: scratch and mouth). For 30 trials of each behaviour, the BS signal was sounded and the monkey received a food reward if the corresponding behaviour was performed. After a 3-second delay the RE signal was given, and if the target behaviour was repeated correctly, the monkey received a second food reward. Immediately after the second reward, another 3-second delay occurred, and the experimenter sounded the RE signal for a second time, noting if the target behaviour was performed, and rewarding the monkey accordingly. Successful performance on the second repeat command is more likely to be based on a memory trace of the behaviour itself rather than of the BS signal, because the latency between the second RE signal and first repeat motor behaviour is shorter than the latency between the second RE signal and the original BS signal. To control for the possibility that the monkeys were spontaneously repeating the target behaviour for a second time, the remaining 30 trials for each behaviour were identical to those described, except that after rewarding the monkey following the first RE signal and a 3-second delay, the experimenter noted if within the next 10 seconds the target behaviour was repeated (with no RE signal being given). Trials were separated by 20-second inter-trial intervals.

2.10.3. Test 2.3.

Over three test sessions the monkeys received 30 trials of the scratch signal followed by the RE signal, and 30 trials of the groom signal followed by the RE signal in random order (Charlie: scratch and mouth). In addition, 30 trials for each target behaviour were administered in which the BS signal was given but terminated after ca. 3 seconds and a food reward was then immediately given to the monkeys, so that they heard the BS signal but did not perform the target behaviour. After a 3-second delay, the RE signal was given and if the target behaviour was performed, a second food reward was given to the monkeys. Trials were separated by 20-second inter-trial intervals. Successful repetition performance should therefore be based on the memory of the target signal, because the target behaviours were not performed and therefore could not serve as a basis for repetition.

2.10.4. Results

2.10.4.1. Test 2.1.

Alcatraz repeated both spontaneous target behaviours as well as both prompted target behaviours significantly above chance (chance = 25%, binomial tests: all $p<0.001$), which indicates that he remembered the motor behaviours of the target episode rather than the BS signals (Figure 2.7). Charlie repeated spontaneous and prompted scratching behaviours significantly above chance (chance=25%, binomial tests: $p<0.001$), but he never spontaneously engaged in mouthing behaviours, which complicates any interpretations of his repetition of the scratching behaviour. Rather than repeating the last behaviour performed, an alternative strategy might have been to scratch on all repeat occasions regardless of the target episode. Therefore, Charlie's repeat-scratch performance cannot be conclusively attributed to his memory of the behaviour itself.

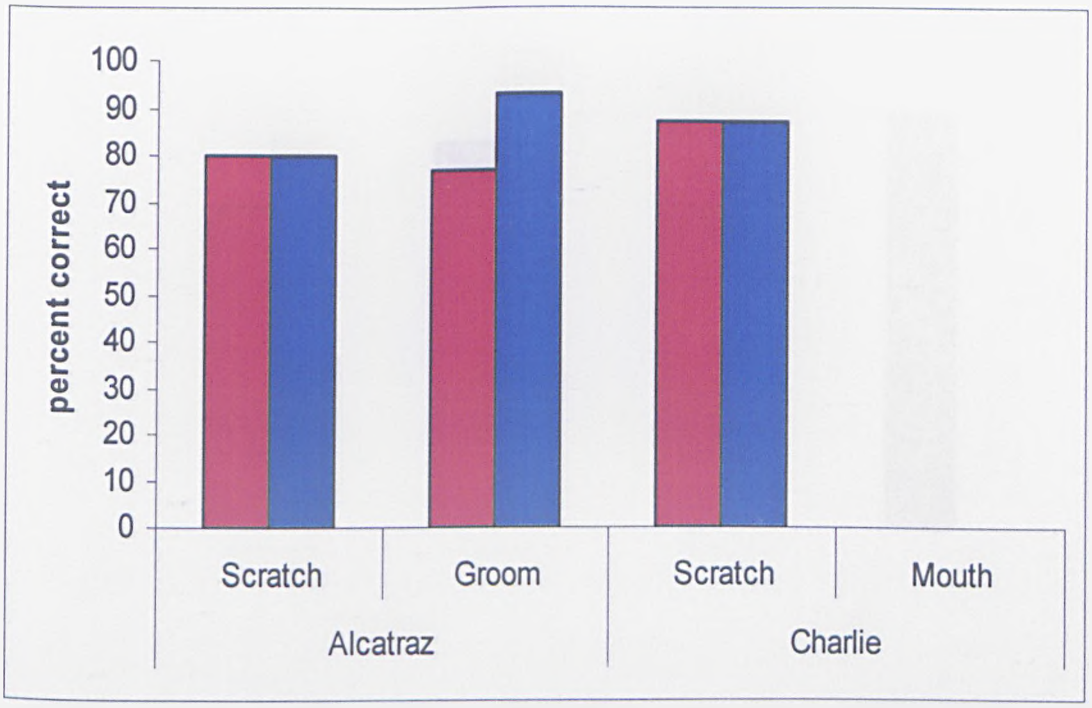

Figure 2.7. Test for multiple memory dimensions. Percentage of correct repetitions for two target behaviours presented for Alcatraz and Charlie during Test 2.1. Red bars = repetition with RE signal; blue bars = repetition with RE signal following spontaneous behaviour.

2.10.4.2. Test 2.2.

As Figure 2.8 shows, both monkeys repeated the target behaviour significantly above chance (chance=25%, binomial tests: $p<0.001$) after hearing the RE signal. Repetition was not different from chance levels when no RE signal was sounded, indicating that the repetition was prompted by the RE signal. The results of Test 2.2 confirm the results of Test 2.1 and suggest that both monkeys remembered their behavioural motor output rather than merely the BS signal for target episodes.

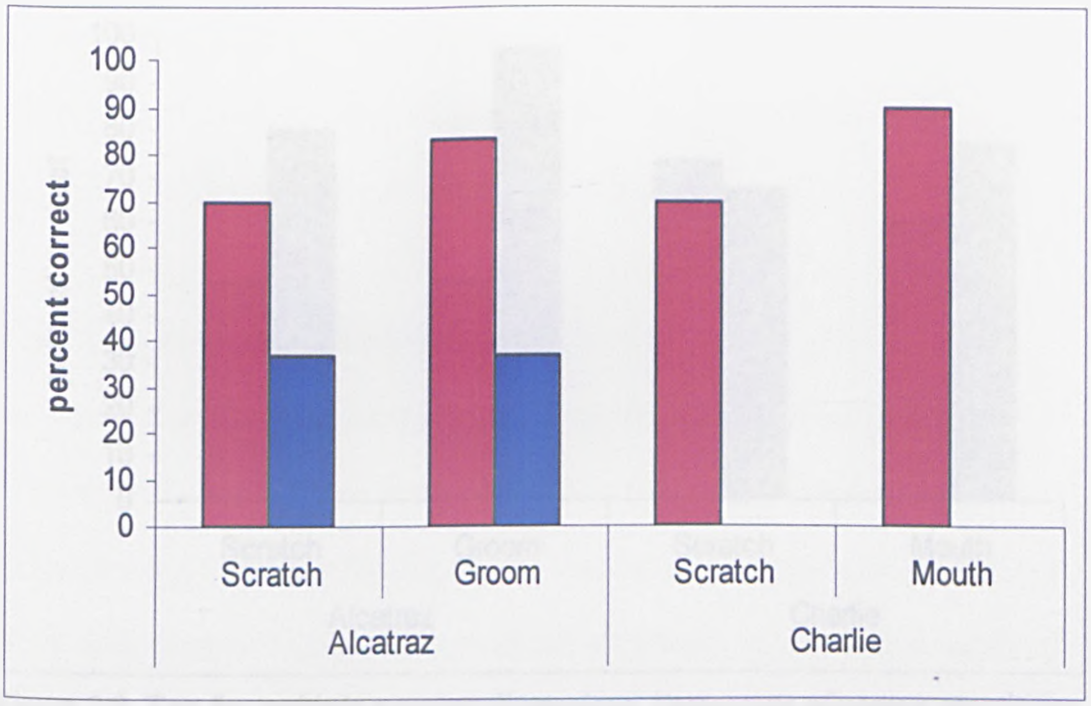

Figure 2.8. Test for multiple memory dimensions. Percentage of correct repetitions for two target behaviours presented for Alcatraz and Charlie during Test 2.2. Red bars = repetition with RE signal; blue bars = repetition without RE signal.

2.10.4.3. Test 2.3.

As illustrated in Figure 2.9, both monkeys performed the target behaviour significantly above chance after hearing the RE signal, even when they did not initially perform the target behaviour (chance=25%, binomial tests: p<0.02). However, their performance in these types of trials was less accurate than when they were allowed to perform the target behaviour (chance=25%, binomial tests: p<0.001). An explanation might be that the duration of the signal affected the monkeys' repetition performance. The BS signal in Test 2.3 was shorter than in other training or test trials, and as a result might have left weaker memory traces.

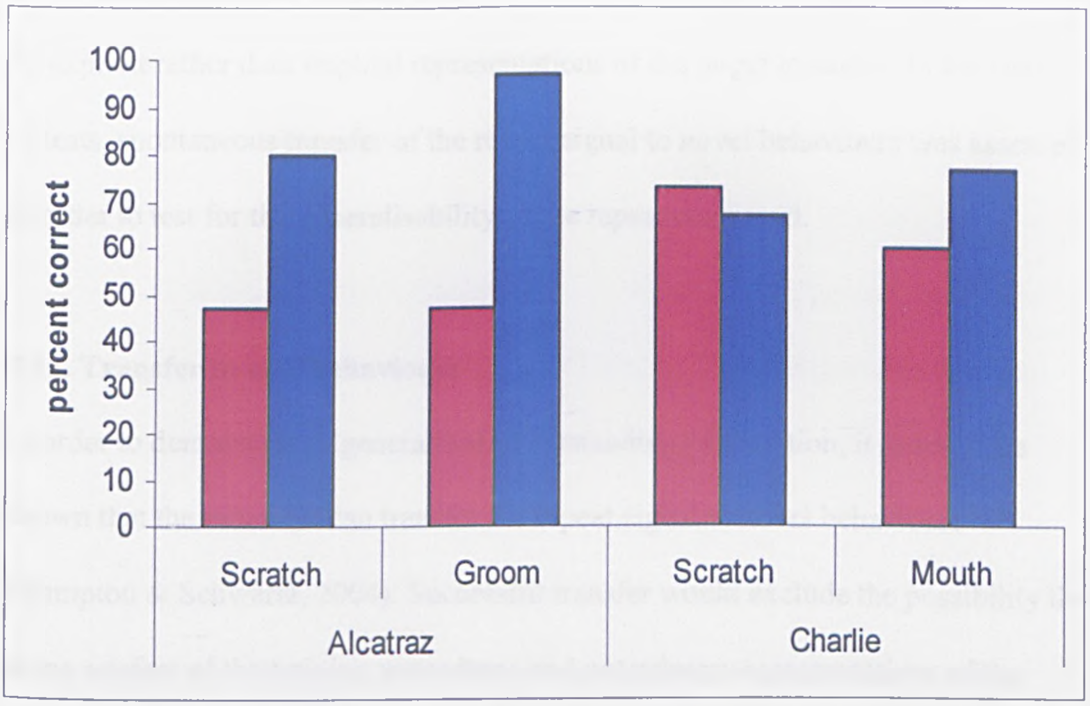

Figure 2.9. Test for multiple memory dimensions. Percentage of correct repetitions for two target behaviours presented for Alcatraz and Charlie during Test 2.3. Red bars = repetition with RE signal following BS signal without target behaviour performed; blue bars = repetition with RE signal.

2.10.5. Discussion

Results of Tests 2.1-2.3 show that both monkeys repeated the target behaviour after performing it in the absence of the behaviour-specific signal (Tests 2.1 and 2.2), and also after hearing the behaviour-specific signal without engaging in the target behaviour (Test 2.3). Even though Charlie's performance in Test 2.1 could not be conclusively attributed to his memory of motor outputs due to an absence of spontaneous mouthing behaviours, the results of Test 2.2 suggest that he remembered the motor output rather than the BS signal. These tests demonstrate that the monkeys are capable of remembering at least two distinct mnemonic elements of the target episode, the behavioural signal and the motor output. Together these results suggest that the monkeys based their repetition performances on explicit rather than implicit representations of the target episodes. In the next set of tests, spontaneous transfer of the repeat signal to novel behaviours was assessed in order to test for the generalisability of the repeat command.

2.11. Transfer to new behaviours

In order to demonstrate a generalised understanding of imitation, it needs to be shown that the monkeys can transfer the repeat signal to novel behaviours (Hampton & Schwartz, 2004). Successful transfer would exclude the possibility that some artefact of the training procedures and not primary representations of the target episode led to correct repetition performance. To test if the monkeys could correctly respond to the RE signal in combination with novel, unexpected behaviours, two transfer tests were conducted. Test 2.4 applied the RE signal to the third trained behaviour, which was never combined with the RE signal during training. Test 2.5 tested the transfer of the RE signal to new, untrained behaviours. Successful transfer to new behaviours would be confirmatory evidence that the monkeys were basing their repetition performances on primary representations.

2.11.1. Test 2.4.

Over three sessions, both monkeys received 30 scratch signals followed by RE signals, and 30 groom signals (Charlie: mouth) followed by RE signals. The crucial test trials of 30 mouth signals (Charlie: groom) followed by RE signals were randomly interspersed among these other trials. To ensure that repetition was prompted by the RE signal, both monkeys also received 30 trials each of scratch, groom and mouth BS signal followed by a 10 second observation period in the absence of the RE signal. Trials were separated by 20-second inter-trial intervals.

2.11.2. Test 2.5.

Two new (untrained) behaviours were selected for Test 2.5 based on observations of frequent spontaneous occurrences of these behaviours, namely yawning for Alcatraz and vocalization (coo-calls) for Charlie. Both of these behaviours can be operantly conditioned (Louboungou & Anderson, 1987; Pierce, 1985), suggesting that they are at least partially under voluntary control of the monkeys and therefore suitable for transfer assessments. Both monkeys were again observed in their home cages. When a target behaviour occurred, the monkey received a food reward, followed by a 3-second delay. On half the trials, the RE signal was given, and if the monkey repeated the target behaviour he received a second food reward. On the remaining trials the monkey was simply observed for a further 10 seconds, and any occurrences of the target behaviour were noted. Test sessions lasted for 30 minutes, with the types of trials alternating for each monkey. Alcatraz was tested over four sessions and received 22 trials with and 23 trials without the RE signal. Charlie was tested over 2 sessions and received 30 trials with and 30 trials without the RE signal.

2.11.3. Results

2.11.3.1. Test 2.4.

Figures 2.10 and 2.11 show that both monkeys repeated the trained behaviours significantly above chance in response to the RE signal (chance=25%, binomial tests: $p<0.001$), but not in the absence of the RE signal. Alcatraz (Figure 2.10) repeated all three target behaviours more often during trials with the RE signal compared to trials without the RE signal, including the transfer behaviour mouthing

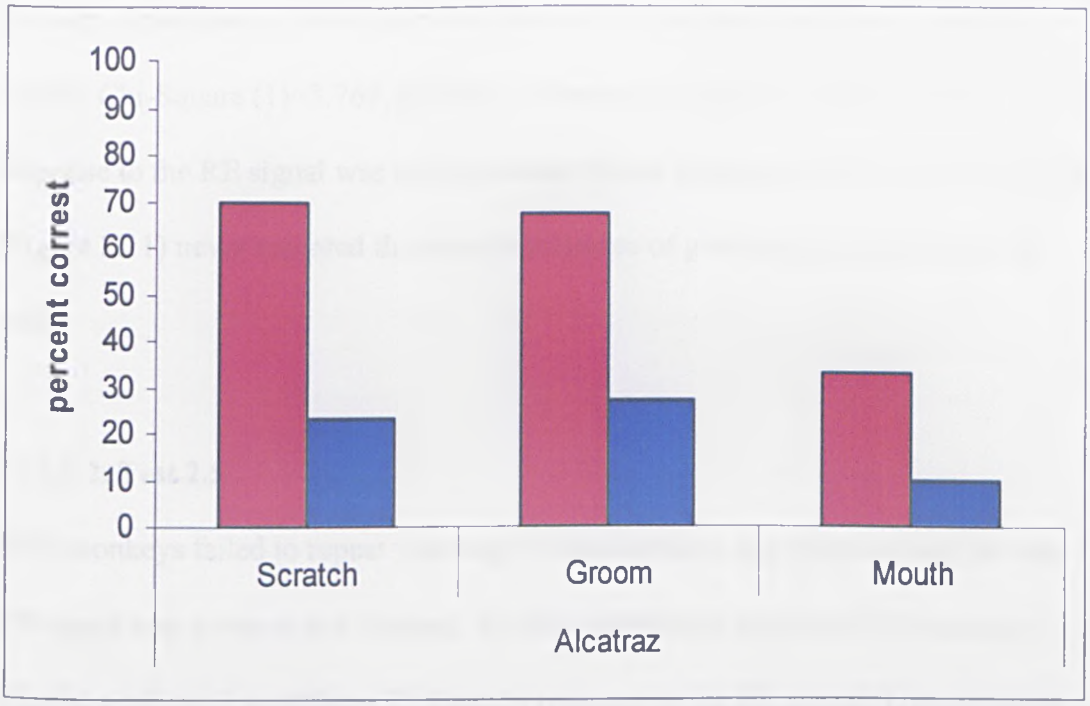

Figure 2.10. Transfer tests to new behaviours. Percentage of correct repetitions for three target behaviours for Alcatraz. Red bars = repetition with the RE signal, blue bars = repetitions without the RE signal.

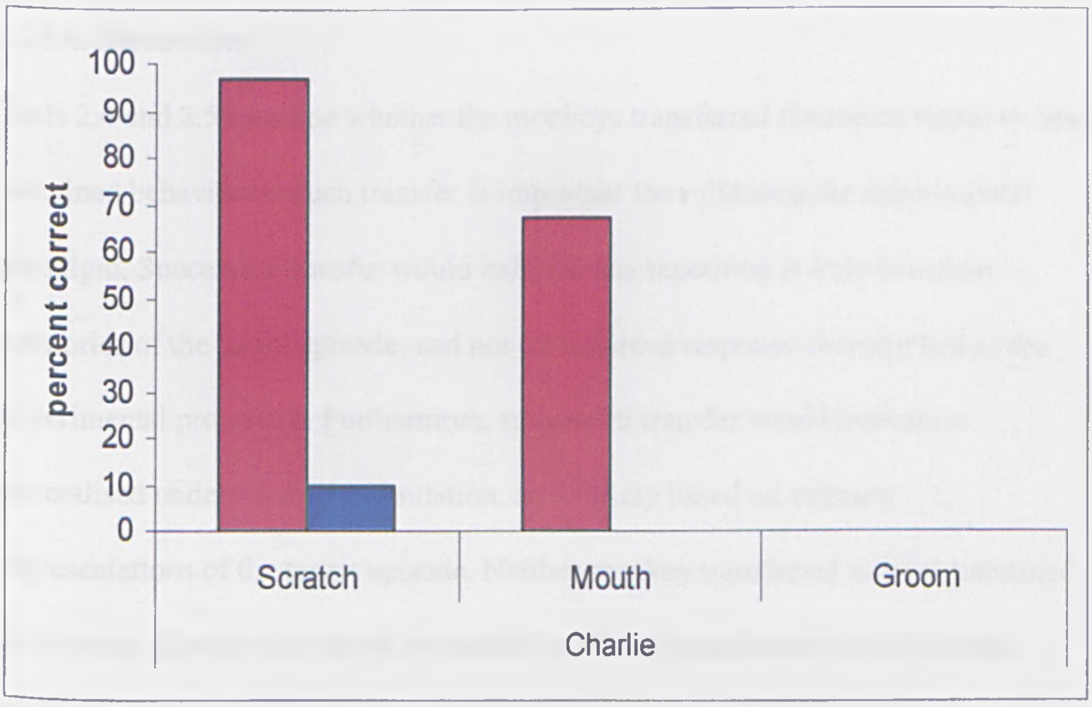

Figure 2.11. Transfer tests to new behaviours. Percentage of correct repetitions for three target behaviours for Charlie. Red bars = repetition with the RE signal, blue bars = repetitions without the RE signal.

(scratch: Chi-Square (1)=7.0, p=0.008; groom: Chi-Square (1)=5.143, p=0.023; mouth: Chi-Square (1)=3.769, p=0.052). However, repetition of mouthing in response to the RE signal was no better than chance (binomial test: p>0.05). Charlie (Figure 2.11) never repeated the transfer response of grooming on either type of trial.

2.11.3.2. Test 2.5.

Both monkeys failed to repeat yawning or vocalizations, regardless of whether the RE signal was given or not. Instead, Alcatraz performed scratching 12 times and Charlie performed scratching 29 times in response to the RE signal. This complete absence of successful repetitions strongly suggests that the monkeys failed to transfer the repeat signal to this new context.

2.11.4. Discussion

Tests 2.4 and 2.5 assessed whether the monkeys transferred the repeat signal to new, untrained behaviours. Such transfer is important for validating the experimental paradigm. Successful transfer would indicate that repetition is truly based on memories of the target episode, and not a reinforced response strongly tied to the experimental procedure. Furthermore, successful transfer would indicate a generalised understanding of imitation, most likely based on primary representations of the target episode. Neither monkey transferred to new, untrained behaviours; Charlie also failed to transfer to other trained behaviours, whereas Alcatraz showed some indication of transfer to one trained behaviour.

Previous research has shown that monkeys can learn abstract concepts, but that the size of the stimulus set may be a critical factor in the acquisition of these concepts. For example, Katz, Wright & Bachevalier (2002) trained rhesus monkeys to make same/different judgments using 8-, 16-, 32-, 64- or 128-item sets of pictorial stimuli, and found no transfer to novel items after 8-item set training but good transfer to novel items after 128-item set training. This result suggests that rather than relying on trial-and-error learning, monkeys with extensive experience of applying an abstract concept to a variety of situations are more likely to understand and use an abstract rule in a novel situation (see also the transfer index (TI) methodology; Rumbaugh & Pate, 1984).

Katz et al.'s (2002) findings make it likely that the monkeys in the present study did not form an abstract concept of the repeat signal based on its application to only two behaviours during training. It seems possible that the monkeys learned the correct repetition of the trained behaviours via rote-learning, e.g. to scratch if the previous behaviour was scratching, groom if the previous behaviour was grooming, etc. Application of rote-learning implies that repetition <u>was</u> based on memory of the previously performed behaviour, and that the absence of full transfer might have been caused by constraints in their abstract learning abilities. It remains possible that the monkeys can fully transfer the repeat signal to novel contexts after a sufficient variety of applications during training.

Having established that repeat performance was based on at least primary representations, further assessments were necessary to infer secondary representational abilities. As described above, a n-back version of the repeat task would be a strong indicator for secondary representational abilities. In order to achieve a n-back task, it was first necessary to establish that monkeys could successfully repeat the target behaviour with extended delays between the target behaviour and the repeat signal. In this third stage, the monkeys' ability to recall target behaviours from long-term memory was assessed.

2.12. Increasing the delay period between target episode and repeat signal

In this final test series, the delay between the target behaviour and RE signal was increased to explore how long the monkeys are able to retrieve a memory of the target episode. Test 2.6 increased the delay between BS signal and RE signal from 3 seconds to 10 seconds. In Test 2.7, the delay was increased to 30 seconds.

2.12.1. Test 2.6.

The monkeys received a total of 120 trials administered in random order over three test sessions. Thirty trials consisted of the scratch signal followed by the RE signal after a 10-second delay, and 30 trials consisted of the groom signal followed by the RE signal after a 10-second delay. To control for random repetitions of the target behaviours following the delay period, 30 trials of the scratch signal and 30 trials of the groom signal were given which were followed by a 10-second observation period in the absence of the RE signal (Charlie: scratch + mouth). Trials were separated by 20-second inter-trial intervals. As for previous tests, chance performance was defined as correct repetition on 25% of trials.

2.12.2. Test 2.7.

Test 2.7 was identical to Test 2.6, except that the delay between BS signals and RE signals was increased to 30 seconds.

2.12.3. Results

2.12.3.1. Test 2.6.

Alcatraz repeated both target behaviours significantly above chance with a delay of 10 seconds between target behaviour and RE signal (chance=25%, binomial tests: $p<0.001$). With the same delay period, Charlie repeated mouthing but not scratching significantly above chance (chance=25%, binomial tests: $p<0.001$; Figure 2.12). On scratching trials, Charlie showed a significant bias for mouthing after hearing the RE signal (21 trials out of 30, binomial test: $p<0.001$). Charlie's mouthing repetitions therefore seemed to stem from a generalized tendency for mouthing upon hearing the RE signal after a delay of 10 seconds, rather than from memory of the target behaviours. For both monkeys, target behaviours were triggered by the RE signal itself and did not occur by chance, as shown by trials without the RE signal, in which target behaviour occurred below chance levels.

2.12.3.2. Test 2.7.

At 30 seconds delay, Alcatraz continued to repeat the scratching response significantly above chance (chance=25%, binomial tests: $p<0.001$; Figure 2.13). However, correct grooming repetitions fell to chance levels, and Alcatraz showed a bias for scratching in response to the RE signal (19 trials out of 30, binomial test: $p<0.001$). Therefore, Alcatraz apparently failed to recall the target episodes at 30

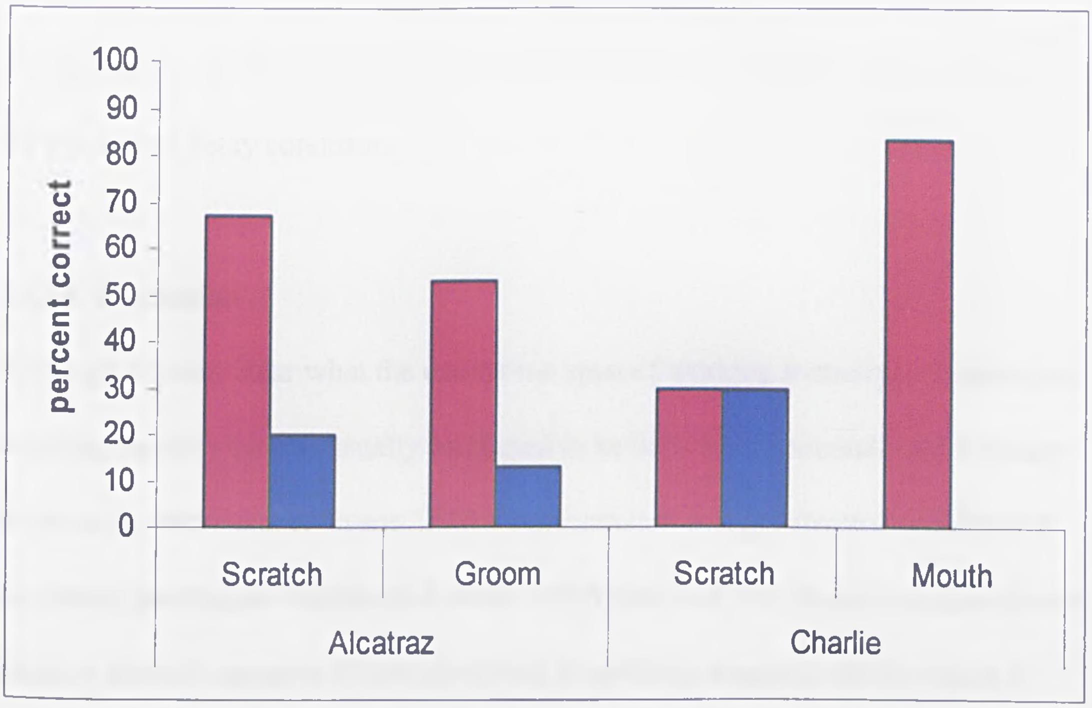

Figure 2.12. Increase in delay between BS and RE signal. Percentage of correct repetitions for two target behaviours at 10-second delay. Red bars = repetition with the RE signal, blue bars = repetitions without the RE signal.

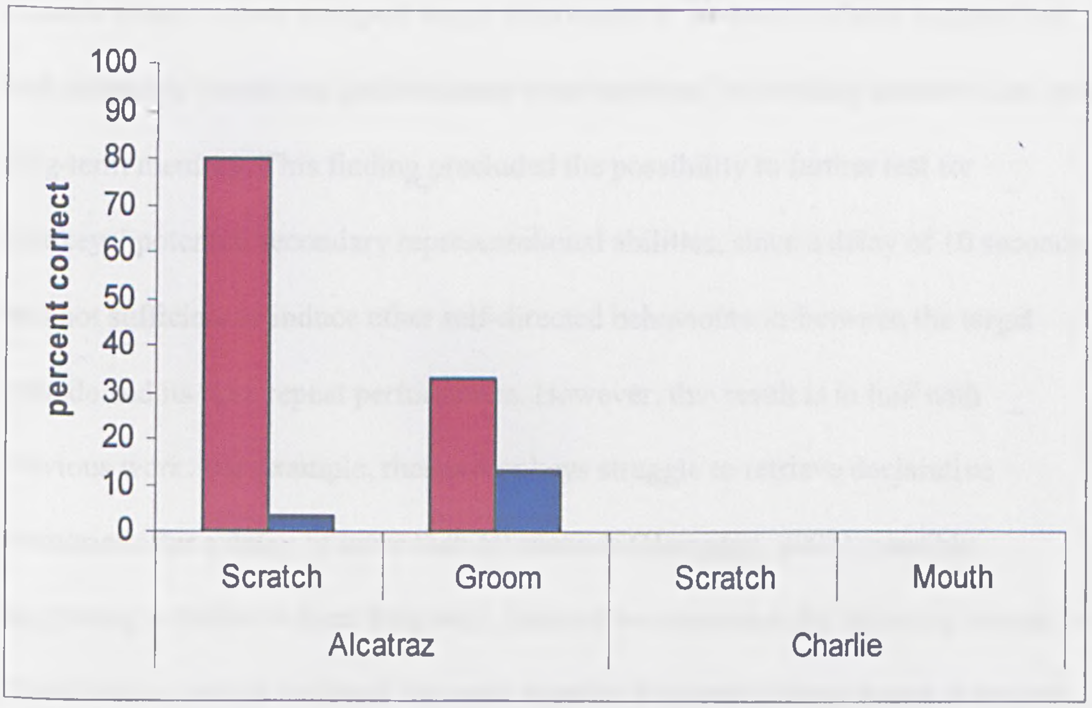

Figure 2.13. Increase in delay between BS and RE signal. Percentage of correct repetitions for two target behaviours at 30-second delay. Red bars = repetition with the RE signal, blue bars = repetitions without the RE signal.

seconds delay. As Charlie failed the 10-second delay condition, he was not tested in the 30-second delay condition.

2.12.4. Discussion

Although it is not clear what the exact time span of working memory is in monkeys, working memory span is usually estimated to be between 30 seconds and 1 minute in primates (Schwartz & Evans, 2001). Furthermore, using distractor and directed forgetting paradigms Washburn & Astur (1998) showed that rhesus monkeys do not seem to actively rehearse information held in working memory, which makes it likely that information recalled after a 1-minute delay is retrieved from long-term memory. In the current study, one monkey could repeat target behaviours at a delay of 10 seconds; however, neither monkey could repeat target behaviours at 30 seconds delay. Failure to repeat target behaviours at 30 seconds delay suggest that both monkeys' repetition performances were mediated by working memory, and not long-term memory. This finding precluded the possibility to further test for monkeys' potential secondary representational abilities, since a delay of 10 seconds was not sufficient to induce other self-directed behaviours in-between the target episode and its later repeat performance. However, this result is in line with previous work. For example, rhesus monkeys struggle to retrieve declarative memories after a delay of more than 60 seconds (Hampton, 2001), possibly suggesting a failure to form long-term declarative memories. By inducing lesions in rhinal cortex, medial temporal lobe and superior temporal lobe in rhesus macaques, Fritz, Mishkin & Saunders (2005) found that long-term memory for auditory stimuli was impaired with lesions in the superior and medial temporal lobe, but not the in rhinal cortex. Lesions in the rhinal cortex are known to impair long-term memory in rats, hence the finding that lesions in monkeys' rhinal cortex do not affect auditory memory suggests that monkeys may not be capable of placing auditory traces into their long-term memory (Fritz et al., 2005). In addition, Hampton et al. (2005) showed that rhesus monkeys are sensitive to the type and location of food items, but fail to remember when they acquired knowledge about these food items. Hence, the monkeys' failure to retrieve primary representations from long-term memory confirms previous results and precludes the possibility for further assessment of secondary representational abilities within this paradigm.

2.13. General Discussion and Conclusion: Self-imitation and secondary representations in monkeys

Two monkeys were trained to perform three self-directed behaviours, and to repeat two behaviours in response to a 'repeat' signal. It was argued that primary representations of the performed behaviours might underlie correct repetition performance, and the nature of these representations was examined. In particular, multiple memory dimensions and transfers to novel behaviours to confirm primary representations of the target episode were assessed. Both monkeys showed evidence of multiple memory elements, which suggests that primary representations were underlying correct repetition performance. In terms of transfer to novel behaviours, neither monkey showed spontaneous transfer to novel, untrained behaviours, although one monkey showed partial transfer to a novel, though previously trained behaviour. However, other factors (such as difficulties to form abstract concepts of the repeat command based on a small sample of applications) may also explain the failures of transfer. Hence, it seems reasonable to conclude that the monkeys' repeat performance relied on explicit primary representations of the target episode.

A further test attempted to assess the monkeys' ability to recall primary representations from long-term memory. As argued above, secondary representations can be inferred if a model's actions are (i) explicitly represented, (ii) can be drawn upon in the absence of the model, and (iii) can be replicated even when other input was received from the model in-between the act of witnessing and executing the imitative act. Whilst (ii) is inherent to the repeat paradigm and (i) was achieved through Tests 2.1-2.3, long-term recall of the target behaviour is required in order to demonstrate (iii). As both monkeys failed to repeat their own behaviours after a 30-second delay, they seem to have utilised their working memories for this task, but failed to show long-term retention. This finding does not suggest that monkeys do not have any long-term memory at all, however considering Fritz et al.'s (2005) findings, monkeys may have impaired long-term memories for auditory stimuli. Unfortunately due to time pressures, additional training on long-term recall was not possible. Hence, even though secondary representational abilities could not be assessed in the present paradigm, the prerequisites for a n-back test were not favourable to assume that monkeys might succeed in it. This finding suggests an absence of secondary representational abilities in this monkey species.

2.14. Self-imitation and imitation paradigms

This paradigm of repeating one's own behaviour has been dubbed a 'self-imitation' paradigm, and it appears to draw upon primary representational abilities. However, if primary representations indeed underlie both 'self-imitation' and imitation, one could ask why monkeys appear capable of imitating themselves to some extent but not capable of imitating others. One solution to this apparent inconsistency might be that imitating others relies on additional abilities which may be beyond monkeys' cognitive capacities. For example, monkeys' imitative abilities might be hampered by motivational factors, inability to attend to the relevant behaviours of the model, limited inhibitory control of non-relevant actions, or other factors inherent to the social context of imitation. The present results suggest that it is not a failure to form primary representations that prevents monkeys from imitating others, but perhaps one or more of these other factors.

2.15. The repeat paradigm and episodic memory

Long-term retention of explicit representations is also interesting from the point of episodic memory abilities. Tulving (1972) defined episodic memory as a long-term declarative memory system that is involved in the recollection of individual events from one's personal past. Episodic memory contrasts with semantic memory in that the former is an autobiographical recollection that is bound into a framework of time and space (Baddeley, 2001), whereas the latter holds generic knowledge about the world. Episodic memories are characterized by a "re-living" of the past (Tulving, 1985), and therefore have a phenomenological, 'autonoetic' (self-referential) quality (Wheeler, Stuss & Tulving, 1997). This "mental time-travel" aspect has become one of the most distinguishable features of episodic memory compared to other memory systems (Tulving, 1998).

The question of whether animals have episodic memories has become a hotly debated topic amongst psychologists. Although theoretical arguments have been around for over 20 years, with some cognitive psychologists claiming that episodic memory abilities are uniquely human (e.g. Tulving & Markowitsch, 1998; Conway, Campbell & Gathercole, 1995; Suddendorf & Corballis, 1997), comparative psychologists have recently turned their attention to this issue, and have begun to look for empirical evidence of episodic memory abilities in nonhuman animals. Some claim to have positive evidence (e.g. in scrub jays: Clayton & Dickinson, 1998), others have found no evidence (e.g. in rats: Bird, Roberts, Abroms, Kit & Crupi, 2003). As our closest living relatives, primates might seem the most likely candidates to share our episodic memory abilities, but so far reports of episodic memory in primates available are not conclusive (Schwartz & Evans, 2001).

According to Perner (1990; 1991; 2001), episodic memory abilities are based on metarepresentations. Unlike secondary representations of the past, episodic memory is experienced as a representation of the past. In other words, it is the mental time travel experience requiring an individual to conceive of the secondary representation of the past experience as personally experienced, which makes episodic memory metarepresentational (see also Perner, 1990). As such, episodic memory abilities would not only indicate secondary representational abilities, but also metarepresentational abilities.

Most attempts to assess episodic memory in animals to date are problematic to interpret because recognition paradigms have been employed (see Schwartz & Evans, 2001). Therefore, most of the relevant animal studies might not have been able to unequivocally distinguish episodic memory from familiarity processes. One exception perhaps is Menzel's (1999) study of a language-trained chimpanzee, who could indicate on a keyboard to a naïve trainer what items had been hidden in its outside enclosure the day before (hence combining memories of what (object), where (location) and when (previous day or earlier). Even though this paradigm combines long-term recall with a what-where-when structure, it remains questionable to what extent it requires "re-living" of the past event. At the very least it appears to be based on secondary representational abilities. To date there is only one study looking at episodic memory in monkeys using a paradigm based on Clayton & Dickinson's (1998) what-where-when experiments, and it failed to find evidence for this ability in rhesus macaques (Hampton et al., 2005). The results of the present study further suggest that monkeys also fail to remember primary representations for extended periods of time, which raises the question whether monkeys' failure to show episodic memory abilities is based on a failure to form metarepresentations, or whether it can more accurately be attributed to a failure to form lasting primary representations. Future work on monkeys' representational abilities might provide an answer to this question.

Despite failing to find evidence for secondary representational abilities in the present experiments, the repeat paradigm may nonetheless prove useful in the assessment of episodic memories in non-verbal species. First, it is based on subjects' recall ability so that subjects cannot use familiarity cues in their immediate environment to repeat a target behaviour. Most episodic memory paradigms for animals have used recognition paradigms, which confound these familiarity aspects with episodic memory processes (Schwartz & Evans, 2001). Second, it does not rely on verbal abilities, making it ideally suited for animal research. Third, perhaps unlike other non-verbal tests of episodic memory, it should be relatively easy to verify whether this paradigm indeed taps into episodic memory. Human patients with specific brain damage resulting in the loss of episodic memory (e.g. patient K.C.; Tulving, 2005) could be asked to repeat a self-directed behaviour after variable delays. Failure to repeat the target behaviour would indicate that episodic memory is a necessary requirement of repetition performance, whereas successful repetition of the target behaviour would imply a solution through other memory mechanisms. Even though the paradigm itself does not allow for a direct measure of 'mental time-travel' experience from our nonhuman subjects, validation on human patients would make a strong case for episodic memory abilities underlying cued behavioural repetitions after extended delays.

Chapter summary

This chapter reports an experiment on self-imitation in pig-tailed macaques, in which self-directed behaviours were repeated following a neutral repeat signal. It is argued that repeat performance is based on primary representations as shown by successful repetition on the basis of two distinct mnemonic aspects, and partial transfer of the repeat signal to two novel behaviours by one monkey. It was then reasoned that successful performance on a n-back version of the repeat task can be seen as evidence of secondary representations of the target behaviour, and in order to achieve this task, long-term recall of the repeat cue was assessed. Both monkeys failed to retrieve primary representations from long-term memory, which led to the termination of this experiment. It is argued that prerequisites for secondary representational abilities in this species are not favourable, and that other factors besides primary representational abilities may cause the lack of imitation of others found in other studies with monkeys. Despite the negative results reported here, the repeat paradigm is nonetheless deemed useful for the purpose of assessing episodic memory abilities in non-verbal populations.

Chapter 3: Imitation Recognition in Pig-tailed Macaques and Capuchin Monkeys

Having considered self-imitative abilities in pig-tailed macaques in Chapter 2, Chapter 3 looks at imitation recognition in both pig-tailed macaques and capuchin monkeys. Unlike imitating others, very little attention has been paid to the extent to which primates can recognise when they themselves are being imitated. This neglect is unfortunate, as imitation recognition can potentially be based on secondary representational abilities, and is therefore ideally suited to investigate secondary representational abilities. Below, the relationship between imitating others and recognising imitation is outlined; the extent to which imitation recognition appears to be based on secondary representations is discussed; and an experiment investigating imitation recognition in both pig-tailed macaques and capuchin monkeys is presented. The following discussion explores to what degree both species can be judged to utilise secondary representations for imitation recognition, and how imitation recognition might nonetheless be compatible with failure to imitate others.

3.1. Imitation, imitation recognition and secondary representations

To recap, imitation can be defined as "the process of accessing a mental representation of an experienced event to reproduce that event through one's own behaviour" (Herman, 2002, pp.66). In other words, when attempting to imitate others, the imitator needs to hold the visual input of another individual's action in mind, and use this representation as a mental model for replicating the demonstrated actions using its own motor output. Therefore, one necessary requirement for imitating others appears to be a mechanism that can match observed actions with actions to be executed by oneself.

Recognising imitation appears to require a similar mechanism, in that it implies that a movement performed by an imitator is recognised as the same movement that the individual being imitated has performed. In other words, the individual has to form a representation of its own performed behaviour, and match the subsequent visual input of the imitator's behaviour to this representation. Both phenomena, imitating and recognising imitation, therefore rely on detecting the equivalence between the actions oneself and another individual perform (Nadel, 2002), and require at least primary representational abilities (see also Chapter 2).

Nadel (2002) distinguished at least two levels of representational complexity at which imitation can be recognised. The more basic level of imitation recognition involves a capacity to recognise structural and temporal contingencies of one's own and an imitator's action, without attributing imitative intentionality to the imitator. This basic ability appears to be achieved through primary representations of one's own actions matched with the imitator's actions, as it consists of a mere perceptual match between actions. A more advanced level of imitation recognition additionally appreciates the imitator's intention to imitate one's own actions (Suddendorf & Whiten, 2001; Suddendorf, 1999). This level of understanding appears to involve the use of secondary representations, since it involves the representation of another individual's intentions or goals (Perner, 1991).

Nadel (2002) further suggested that the representational complexity of imitation recognition can be determined by observing the imitatee's behaviour. Recognition of structural and temporal contingencies might result in a visual discrimination of an imitator compared to a non-imitator. Recognising the imitator's intention to imitate one's own behaviour might also lead to the imitatee testing the behavioural contingencies (such as suddenly changing its movements while looking at the imitator), and (at least in humans) increased social responses toward the imitator, such as smiling and laughing (Nadel, 2002). Tests of contingency show that the imitatee appreciates the imitator's intentions by trying to disrupt the predictability of the own behavioural patterns; monitoring the effects of these disruptions on the imitator's motor acts might then lead to increased smiling and laughing. Therefore, according to Nadel (2002), the use of primary and secondary representations within imitation recognition abilities can be assessed through visual preferences, social responses and contingency testing behaviours.

3.2. Imitation recognition in human infants

Several studies have examined when humans start to recognise imitation. Meltzoff (1990; 1996) pioneered the study of imitation recognition in humans, and conducted three experiments to assess imitation recognition abilities in 14-month-old infants. In the first experiment, an interesting toy was given to infants who were sitting on their mothers' lap. Each infant was confronted by two experimenters holding identical toys. One experimenter, assigned the role of imitator, imitated the infant's actions with the toy as closely as possible. The second experimenter simply held the toy but remained passive throughout the experiment. The results showed a significant visual preference and significantly more testing behaviours and smiling directed at the imitator. However, one explanation for this preference could be that infants simply preferred looking at an experimenter interacting with a toy, rather than any recognition of imitation as such. A second experiment addressed this issue by having the non-imitator interact with the toy, but performing previous actions instead of the infant's current actions towards the toy. Again, significant visual preferences for the imitator and significantly more testing behaviours and smiling directed at the imitator were found. However, the preference in this second experiment might relate to a preference for temporal contingencies, since the non-imitator's actions were not temporally matched with the infant's actions. Hence this second experiment cannot differentiate whether the infant recognised imitation on the basis of structural contingency, or on the basis of temporal contingency. Therefore in a third experiment, the non-imitator acted at the same time as the imitator but performed pre-determined, non-matching actions. Results of this final experiment confirmed results from the previous two experiments: infants showed a significant visual preference for the imitator as well as significantly more testing behaviours and smiling directed at the imitator.

Meltzoff's (1990; 1996) original findings were replicated by Asendorpf et al. (1996), who found that infants can recognise imitation independently of passing a self-recognition test, but that self-recognisers were more likely to engage in synchronic imitation (i.e. shadowing play with same toys). These findings support the hypothesis that both self-recognition and imitation recognition can be achieved through secondary representations. Agnetta & Rochat (2004) extended Meltzoff's (1990) paradigm by adding a new condition in which either an experimenter imitated the infants' actions with a toy, or the toy mimicked the infants' actions without obviously being controlled by an experimenter (the toy was controlled via a lever underneath the table). Agnetta & Rochat (2004) found that infants differentiated between the experimenter-controlled and the non-experimenter-controlled imitation process. 14 -18 month old infants showed significantly more looking and testing behaviours directed at the imitator compared to the ghost imitation condition. 9-month-old infants did not show preferential testing behaviours directed at the imitator. Thus, human infants appear to recognise imitation as an intentional imitative process from 14 months of age onwards whereas simple imitation recognition abilities appear to be present at 9 months. These emerging patterns fit well with other findings indicating that secondary representational capacities develop between 1-2 years of age (Agnetta & Rochat, 2004).

3.3. Imitation recognition in apes

Only one previous experiment has looked at imitation recognition in nonhuman animals. Nielsen et al. (2004) tested one adult male chimpanzee in four different conditions, in which an experimenter 1) imitated the chimpanzee's actions; 2) performed temporally contingent but structurally different actions; 3) performed temporally and structurally different actions; and 4) did not perform any actions. Nielsen and colleagues did not measure visual preferences, but found that the chimpanzee engaged in three testing behaviours when he was being imitated (e.g. orient towards the imitator, place back of hand on cage, rotate arm, poke finger out of cage, place hand on other part of cage, rotate arm, place hand on cage). No such sequence was observed in any of the control conditions, which was taken as an indication that the chimpanzee recognised that he was being imitated (Nielsen et al., 2004). Testing behaviours directed at the imitator may also indicate that the chimpanzee recognised the imitator's intention to imitate him, hinting at secondary representational abilities in chimpanzees.

3.4. Imitation recognition in monkeys

The finding that chimpanzees can recognise imitation complements previous findings that chimpanzees are regarded to be capable imitators (e.g. Hayes & Hayes, 1952; see also Chapter 2) and therefore thought to be capable of secondary representations (Suddendorf, 1999). On the other hand, monkeys are generally regarded to be incapable of imitating others (Visalberghi & Fragaszy, 2002; see also Chapter 2), perhaps due to a failure to generate secondary representations (Suddendorf, 1999). By testing monkeys' abilities to recognise imitation, their level of representational sophistication can be more thoroughly assessed. Adapting Meltzoff's (1990) method for studying human infants, two experiments were conducted to test a group of pig-tailed macaques and a group of capuchin monkeys for imitation recognition abilities. It was hypothesised that both species might show visual discrimination between an imitator and a non-imitator (suggesting primary representations). If these species also have secondary representational abilities, it is predicted that they might show contingency testing behaviours and social responses preferentially directed at the imitator.

3.5. Imitation recognition in pig-tailed macaques

3.5.1. Subjects and housing

Subjects were 10 pig-tailed macaques (*Macaca nemestrina*), 6 male and 4 female, all captive-born, aged between 4 and 18 years (1 sub-adult, 9 adults, mean 8.6

years) and housed at the Dipartimento di Neuroscienze, Parma. Although all monkeys were housed individually (cage measures: 100x160x100cm), their home cages were part of an interconnected cage system that allowed social interactions between two or more individuals. The monkeys were not food deprived, and received their normal feed several hours before the start of each experimental session. Water was available ad libitum.

3.5.2. Procedure

All monkeys were tested individually in their home cages. A table (measuring 104x80x51cm) was placed in front of the cage and two familiar experimenters were seated behind it, facing the monkey but avoiding direct eye contact in order to minimise any inadvertent influence on the monkey's preferential gazing. A wooden cube (edge=5.5cm) with a small hole drilled into each side was given to each experimenter. A digital video camera placed between the two experimenters recorded all sessions with only the monkey in view, thus allowing blind scoring.

At the start of each test trial, a 5-minute baseline assessment of visual preference was conducted. During this baseline, the monkey could observe both experimenters manipulating their respective cubes with hands and mouth, mimicking common actions of the monkeys towards the object such as biting, twisting, poking at the holes etc. Experimenters were not matched for actions and did not act in synchrony. After the baseline period, an identical cube was placed on the table within reach of the monkey, and the test period started as soon as the monkey contacted the cube. During the 5-minute test period, one experimenter imitated the monkey's cube-directed actions as structurally accurately and temporally contingently as possible, while the second experimenter performed monkey-typical actions that were temporally contingent but structurally different. For example, if a monkey mouthed the cube, the imitator would mouth while the non-imitator might poke at the cube's holes. If a monkey let go of the cube to engage in other activities (such as locomotion, social interactions with other monkeys etc.), both experimenters placed their cubes onto the table and remained still until the monkey contacted the cube again. The identity and position of the imitator was counterbalanced between subjects. At least 24 hours after the first trial, a second trial was conducted with each monkey using an identical set up except that the roles of imitator and non-imitator were reversed between experimenters.

3.5.3. Analysis

All the tapes were digitally analysed (25 frames/second) by a rater blind to the experimental condition, and the number of frames spent looking at each experimenter was recorded. Furthermore, any instances of contingency-testing behaviours and social responses directed at the experimenters were noted. Twenty-five percent of sessions were coded a second time to assess intra-observer reliability; agreement between the two codings was high (Pearson's correlation: $r=0.98$, $p<0.001$). Raw scores from both trials were combined for each monkey and divided by 2, so that the following statistical analyses were conducted on the average time of the two trials each monkey had devoted to looking at imitator and non-imitator.

3.6. Results

3.6.1. Looking behaviour

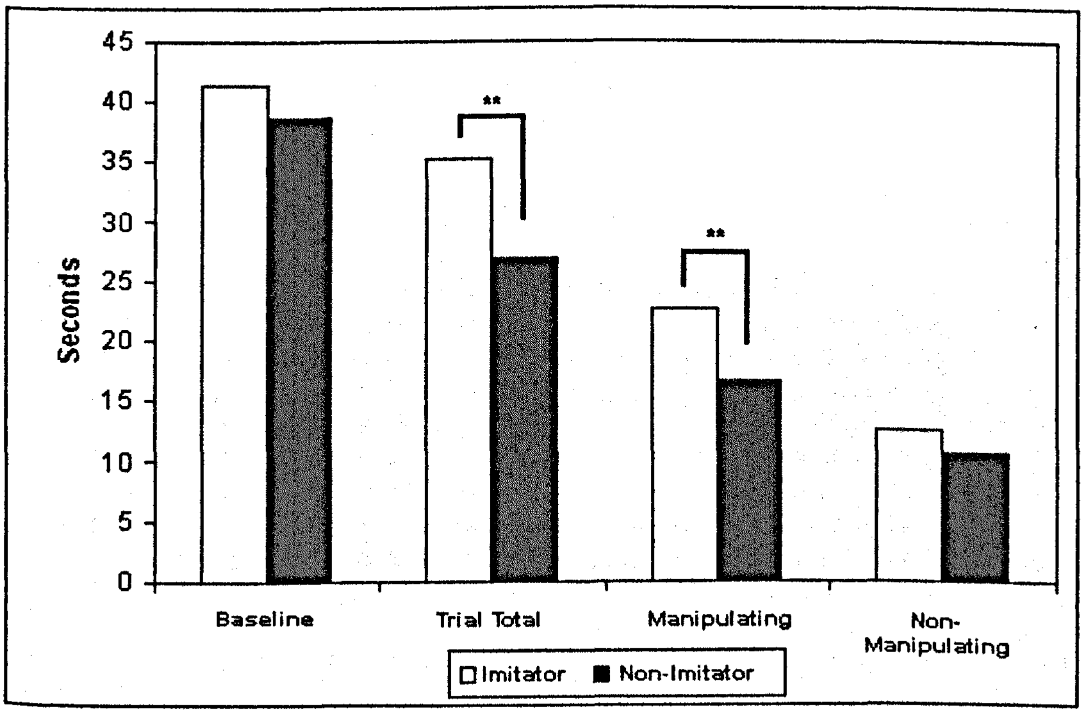

Figure 3.1. Average time in seconds per monkey spent looking at imitator and non-imitator. ** indicates statistical significance with p<0.05.

As Figure 3.1 shows, the macaques showed no significant visual preference for either experimenter during the baseline period, which was confirmed by related sample t-tests (t (9) = 0.946, p>0.05). During the test period, the monkeys' preference shifted and they looked significantly longer at the imitator (t (9) = 2.651, p=0.026).

Since the experimenters only imitated the monkeys' cube-directed actions and not other activities, visual preferences were analysed separately for cube-directed actions compared to all other time periods. Results show that the preference for the imitator was expressed only during manipulation of the cube (t (9) = 2.344, p=0.044), not during non-manipulation (t (9) = 1.988, p>0.05; see Figure 3.1). There was no effect of identity or spatial position (left vs. right) of the imitator, and no difference in the monkeys' looking times between trial 1 and 2 (all p>0.05).

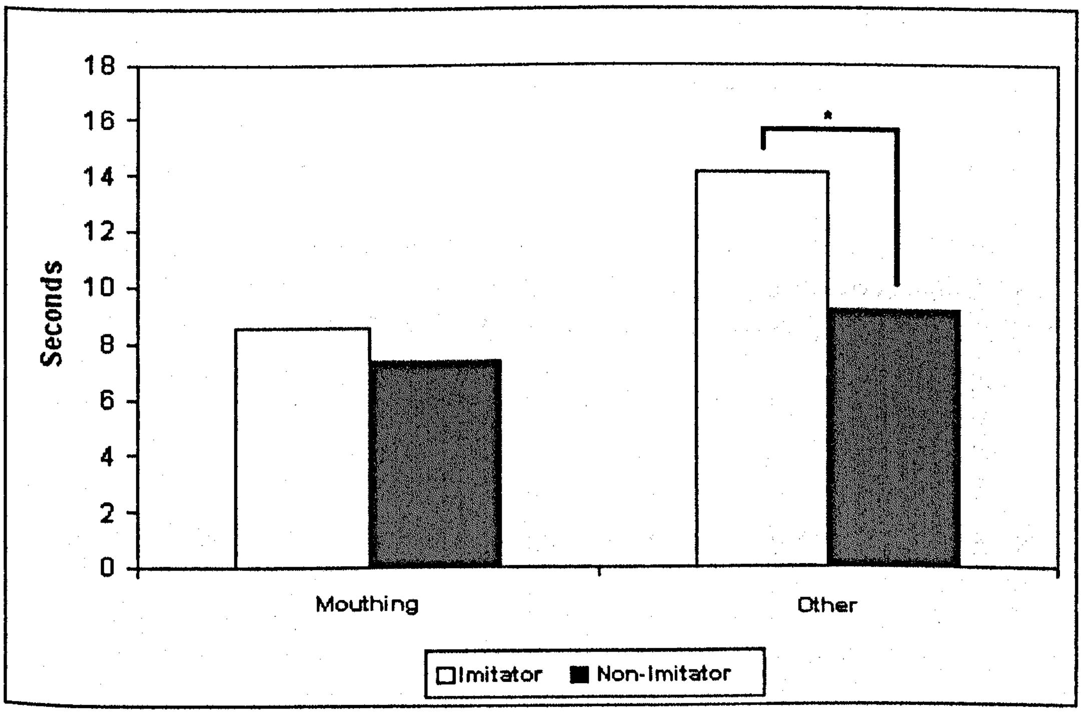

Figure 3.2. Average time in seconds per monkey spent looking at imitator and non-imitator during mouthing and other manipulations. * indicates borderline significance with p=0.051.

All monkeys spent a proportion of each trial mouthing the object, and it could be argued that the monkeys' visual preference might stem from a greater interest in the mouthing action of an experimenter rather than a matching of actions as such. To test this hypothesis, looks towards the experimenters when mouthing and performing other actions were analysed separately. Figure 3.2 shows that when the monkeys were performing other cube-directed manipulations, visual preference for the imitator reached borderline significance (t (9) = 2.255, p=0.051), but no visual preference was found during mouthing (t (9) = 0.877, p>0.05).

As a supplementary analysis, a preferential looking index was calculated which gives a measure of the relative proportion of monkeys looking more at the imitator or non-imitator (see Agnetta & Rochat, 2004). This index was calculated as follows: (imitator - non-imitator) / (imitator + non-imitator). The resulting value represents a preference for the non-imitator if negative, and a preference for the imitator if positive (ranging from –1 to +1). One-sample t-tests were applied to these index values comparing them against zero as chance performance. No significant preference was found during the baseline period (t (9) = 1.105, p>0.05). However, there was again a significant preference during the trial period (t (9) = 3.672, p=0.005), during manipulation of the object (t (9) = 2.532, p=0.032), and in particular, during non-mouthing actions (t (9) = 2.624, p=0.028) but not mouthing actions (t (9) = 0.922, p>0.05).

3.6.2. Contingency testing behaviours

No contingency testing behaviours were observed for any monkey during any phase of the experiment.

3.6.3. Social responses

Eight of the 10 pig-tailed macaques directed at least one social response at an experimenter. In total, 35 pucker responses (compression and protrusion of lips with eyebrows, ears and forehead retracted; Maestripieri, 1996), 61 eye brow raises (affiliative response, scalp and brow retracted, mouth open; Maestripieri, 1996) and 4 fear responses (mouth closed with lips retracted to show teeth; Maestripieri, 1996) were observed. Although there was a significant increase in the number of social responses between baseline and test phase (mean baseline = 1, mean test = 8.7; t (9) =-2.1938, p=0.017), there was no significant difference in the number of social responses directed at imitator and non-imitator during the test phase (mean imitator

= 6.5, mean non-imitator = 2.5, t (9) = 1.766, $p>0.05$). There were also no correlations between age and visual preference or number of social responses (all $p>0.05$).

3.7. Summary: Imitation recognition in pig-tailed macaques

The results of the experiment suggest that pig-tailed macaques recognised when they were being imitated as shown by the significant visual preference for the imitator during the trial period, but not the baseline period. This result is consistent with the hypothesis that this species possesses at least primary representational abilities and discriminates between the imitator and non-imitator on the basis of kinaesthetic-visual and visual-visual matching between their own actions and the experimenters' actions. However, the absence of contingency testing behaviours suggests that the monkeys were not aware of the intentions of the imitator, which requires secondary representational abilities.

3.8. Imitation recognition in capuchin monkeys

3.8.1. Subjects and housing

Subjects were 10 adult tufted capuchin monkeys (*Cebus apella*), 4 male and 6 female, all captive-born, aged between 13 and 26 years (mean 17.7 years) and housed at the Istituto di Scienze e Tecnologie della Cognizione (CNR), Rome. All monkeys lived in social groups of 4-6 individuals in large indoor-outdoor cages (cage measures: $25m^3$ indoor, $22\text{-}25m^3$ outdoor), which could be divided by means of sliding doors. All enclosures were enriched with perches, slides, and wooden and plastic manipulanda. The monkeys were not food deprived, and received their normal diet (monkey chow, fresh fruit and vegetables, seeds and nuts) after each experimental session. Water was available ad libitum.

3.8.2. Procedure

All monkeys were tested individually in their outdoor cages, whilst group members were restrained to the indoor cages. A wooden cube (edge=5.5cm) with a small hole drilled into each side was fastened to the inside of one cage wall by means of a metal chain; two identical cubes with metal chains attached to them but otherwise free for manipulation were given to two experimenters, who stood outside the cage and faced the wooden cube inside the cage. Throughout the experiment, both experimenters avoided direct eye contact with the monkeys in order to minimise any inadvertent influence on the monkeys' preferential gazing. A digital video camera placed between the two experimenters recorded an area of ca. $1m^3$ around the cube within the cage but without the experimenters in view, thus allowing blind scoring.

Unlike the experiment with pig-tailed macaques, the experiment with capuchin monkeys did not allow a measurement of baseline preferences. Only the area around the wooden cube could be filmed for eye gaze analysis, however the monkeys were able to move freely around the large cage in which they were tested. Initial pilot testing showed that the monkeys were highly unlikely to occupy this area without the wooden cube being present. Therefore, only two test trials were run with each monkey. At the start of each test trial, each monkey was released into the outdoor cage and the test period started as soon as the monkey contacted the cube. During the 5-minute test period, one experimenter imitated the monkey's cube-directed actions as structurally accurately and temporally contingently as possible, while the second experimenter performed monkey-typical actions that were temporally contingent but structurally different. If a monkey let go of the cube to engage in other activities (such as locomotion, social interactions with other monkeys etc.), both experimenters placed their cubes onto a table in front of them, and remained still until the monkey touched the cube again. The identity and position of the imitator were counterbalanced between subjects. Forty-eight hours after the first trial, a second trial was conducted with each monkey using an identical set up except that the roles of imitator and non-imitator were reversed between experimenters.

3.8.3. Analysis

All tapes were digitally analysed (25 frames/second) by a rater blind to the experimental condition, and the number of frames spent looking at each experimenter was recorded. Furthermore, any occurrences of contingency-testing behaviours and social responses directed at the experimenters were noted. Twenty-five percent of sessions were coded a second time to assess intra-observer reliability; agreement between both codings was high (Pearson's correlation: $r=0.99$, $p<0.001$). Since the monkeys spent variable amounts of time in the target area, looking times were adjusted to a common time frame of 5 minutes. Scores from the two trials were added for each monkey and divided by 2, so that the following statistical analyses were conducted on the average time in both trials that each monkey spent looking at imitator and non-imitator.

3.9. Results

3.9.1. Looking behaviour

Overall, the capuchin monkeys showed a significant visual preference for the non-imitator throughout the test phase (t (9) = -2.354, p=0.043), suggesting that the monkeys differentiated between the imitator and non-imitator. When further analysing for which periods of the test the preference was most apparent, it emerged that the monkeys did not look significantly longer at the non-imitator during manipulation of the object (t (9) = -1.253, p>0.05), but that there was a trend for a non-imitator preference during non-manipulation of the object (t (9) = -2.135, p=0.062; see also Figure 3.3). This preference for the non-imitator when not manipulating the object appears to be caused by longer looks at the non-imitator (mean=13 frames) compared to the imitator (mean=10 frames, t (189) = -2.006, p=0.046), not by more frequent looks towards the non-imitator (number of looks at imitator=90, number of looks at non-imitator=101, Chi-Square (1) = 0.634, p>0.05).

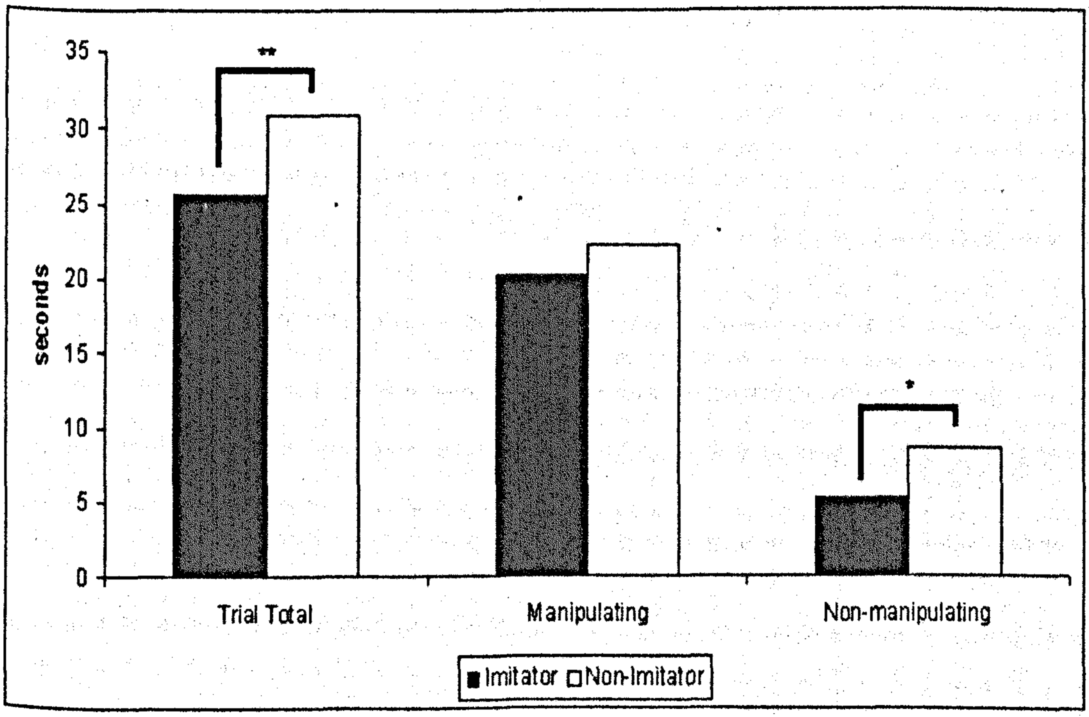

Figure 3.3. Average time in seconds monkeys spent looking at imitator and non-imitator during mouthing and other manipulations, adjusted for time spent in target area. ** indicates significant difference with p=0.043; *indicates trend towards significant difference with p=0.062.

The preferential looking index confirmed the preference for the non-imitator. More monkeys were looking at the non-imitator than the imitator throughout the trial (t (9) = -2.507, p=0.033), mostly due to looking more at the non-imitator during non-manipulation (t (9) = -3.287, p=0.009), not manipulation (t (9) = 1.16, p>0.05). No effects were found concerning identity or spatial position of the imitator, and there was no difference in looking times between trial 1 and 2 (all p>0.05).

3.9.2. Contingency testing behaviours

No contingency testing behaviours were observed for any monkey during any phase of the experiment.

3.9.3. Social responses

Only two capuchin monkeys directed social responses towards the experimenters. One female directed 7 forehead raise (FR; affiliative response, retracting of eyebrows and forehead; Weigel, 1978) responses at the imitator during manipulation bouts, and a total of 20 FR responses at the non-imitator, 16 during manipulation and 4 during non-manipulation. One further female directed one fear response (grin; retracting of forehead and lips, mouth closed, teeth showing; Weigel, 1978) at the imitator during a manipulation bout. Even though these are too few observations to permit statistical analysis, it is noteworthy that in total, more social responses were directed at the non-imitator.

3.10. Summary: Imitation recognition in capuchin monkeys

Capuchin monkeys showed a significant visual preference for the non-imitator during the experiment, which suggests that they differentiated between the imitator and non-imitator. Similar to pig-tailed macaques, this result supports the hypothesis that this species is capable of primary representational abilities and used kinaesthetic-visual and visual-visual matching to recognise the contingency between their own movements and the experimenters' movements. However, the lack of contingency testing behaviours directed at the experimenters also points towards a failure to use secondary representations to conceive of the imitator's intentions to match their own actions.

3.11. General Discussion and Conclusion: Imitation recognition in monkeys

Both pig-tailed macaques and capuchin monkeys differentiated between an experimenter imitating their own actions, and an experimenter acting at the same time but performing different actions, as indicated by significant visual preferences for the imitator (macaques) or non-imitator (capuchins). Since both experimenters acted in synchrony with the monkeys (as much as possible), this preference appears to be based on structural contingency, not temporal contingency, and suggests the presence of at least primary representational abilities. However, why the visual preference should be for the imitator in macaques, but for the non-imitator in capuchin monkeys, is not clear.

Clarifying the mechanism underlying visual preference may be crucial for understanding the monkeys' opposing preferences. Nadel (2002) suggested that imitation is used as a means of communication between human infants and their caregivers, resulting in increased visual attention to the imitator and, if the communication intent is appreciated, social signals directed towards the imitator. These social signals express the infants' pleasure with the communication and serve as a signal to the imitator that the communication is successful. The present experiment found a visual preference and more social responses toward the imitator rather than the non-imitator in macaques. However, the difference for social responses was not significant. In comparison, far fewer social responses were performed by the capuchins, although a visual preference and social responses were both preferentially (albeit non-significantly for social responses) directed toward the non-imitator.

Given that visual preferences and social signals appeared to be preferentially directed at only one experimenter in both species, the data presented here might suggest that both social responses and visual preferences might be related to a common underlying mechanism, which may be an understanding of the experimenter's intentions to communicate. However, such an understanding is thought to lead to contingency testing behaviours (Nadel, 2002) that were not observed in either species in the present experiments. Hence the monkeys appear unlikely to have formed a secondary representational understanding of the imitating experimenter's intention to imitate them, and consequently did not appear to perceive being imitated as a form of social communication. It follows that the monkeys' visual preference and social responses were not an expression of social communication with the imitator, or to use Nadel's (2002) terminology, the monkeys did not form an explicit understanding of imitation recognition.

Nonetheless, visual preference for one experimenter implies at least an implicit understanding of imitation recognition, i.e. recognising structural and/or temporal contingency between own and others' actions. This achievement appears to best describe the monkeys' response patterns. Importantly, whereas communication with the imitator through imitation implies a preference for the imitator, recognising structural and temporal contingencies does not necessarily imply a preference for either experimenter. Subjects may prefer the imitator's familiar actions as observed in the macaques, or the non-imitator's non-familiar actions as observed in the capuchins. Whether the difference in visual preference constitutes a robust species' difference may be explored in further research.

Even though visual preference may be based on contingency recognition, one could wonder why the monkeys directed social responses preferentially at one experimenter. Social responses may not necessarily indicate an understanding of communication but may instead be a consequence of the testing situation. The experimenters were close to the monkeys' cages during testing, and when presented with a novel object the monkeys may have felt threatened by the presence of the experimenters. The fact that more social responses were then directed at one experimenter might simply be a result of the increased visual attention to that experimenter (the imitator for the macaques and the non-imitator for the capuchins). Hence, at least in implicit imitation recognition, visual preference and social responses may be related co-incidentally rather than by means of a common underlying cognitive mechanism.

Although both species were tested using identical methods, several factors outside of the experimenter's control also differed between the two experiments and may have contributed to the observed opposing visual preferences. The macaques were singly housed in relatively small cages with little environmental enrichment available. Capuchins on the other hand were housed in social groups in large, environmentally enriched cages. These different housing arrangements might have led to different approaches to the novel object in the two species. Possibly the experiment provided some environmental enrichment and therefore elicited more interest in the macaques but not the capuchins, which had other forms of enrichment available to them. Consequently, the capuchins generally interacted less with the novel object and engaged in less visual contact with the experimenters throughout the experiment. In addition the macaques were presented with the object outside their cages, whereas the capuchins had direct access to the objects inside their cages. Direct access may have provided better opportunities to quickly explore the object, which may also have resulted in short-lived interest in the object in capuchins. Another potentially contributing factor is the ages of the study animals. The capuchins were on average twice as old as the macaques, which might have contributed to differential task performances. The exact mechanism leading to the species' patterns of preference and how the visual preference and social responses were affected by these additional factors remain to be addressed in future investigations.

3.12. Structures supporting implicit imitation recognition

Implicit imitation recognition appears to be based on explicit representations, in that the monkeys had to form a representation of their own object-directed behaviours and match the visual input of the imitator's behaviour to this representation. Conceivably a single underlying mechanism could match the visual input of one's own actions with visual input of the imitator's actions. Visual-visual matching would also account for the macaques' non-preferential gaze behaviour during mouthing actions, since their own mouthing behaviours are difficult if not impossible to directly observe, and therefore no visual matching of actions could occur during mouthing behaviours. However, other factors might have caused the non-preferences during mouthing behaviours in macaques. For example, macaques frequently used their canines to mouth the object, for which they turned the head to one side. Turning of the head might have resulted in less attention being paid to the experimenters and therefore fewer opportunities to establish a match between actions, which in turn might have led to a failure to establish significant preferences during mouthing behaviours.

Another mechanism that may potentially explain the observed discrimination of imitator and non-imitator involves kinaesthetic-visual matching, i.e. the ability to conceive of the visual form of one's own felt body postures and movements (Mitchell, 2002). Kinaesthetic-visual matching consists of representing the kinaesthetic input of one's own previous behaviour being matched with the visual input of an imitator's actions. Of course, visual-visual matching and kinaesthetic-visual matching need not be mutually exclusive, and macaques and capuchins might have used both mechanisms to recognise imitation. However, visual-visual matching might be expected to manifest itself in quick gaze alternations between the monkeys' own actions and the experimenters' actions in order to establish the necessary visual match between actions. No such successive gaze alternations were observed in either species, thus supporting the kinaesthetic-visual matching hypothesis.

Kinaesthetic-visual matching appears likely to involve mirror neurons, which are found in the ventral premotor area F5 (Rizzolatti, Fadiga, Gallese & Fogassi, 1996) and the inferior parietal cortex of the macaque (Gallese, Ferrari, Kohler & Fogassi, 2002). Mirror neurons discharge both when a monkey performs an action, and when it sees a similar action being performed by an experimenter or another monkey. Area F5 in the macaque brain contains mirror neurons for both hand and mouth actions (e.g. eating or drinking; Ferrari, Gallese, Rizzolatti & Fogassi, 2003). The discharge of mirror neurons when the self is performing an action does not depend on the visual input from the action, as neurons also fire when the monkey executes a hand action without being able to see its hand (Rizzolatti et al., 1996). Mirror neurons therefore have both visual and kinaesthetic properties, and appear ideally suited for kinaesthetic-visual matching.

3.13. Recognising imitation and performing imitation

Finally, if macaques and capuchins both recognise when another individual imitates them, one might wonder why monkeys nonetheless appear to consistently fail to imitate others. Although several forms of social learning have been identified in wild populations (e.g. Panger et al., 2002), researchers now largely agree that monkeys are not capable of true imitation of the type exhibited by the imitator in the experiments presented here (Visalberghi & Fragaszy, 1990, 2002; Galef, 1990; Whiten & Ham, 1992). Several factors potentially preventing imitation execution are conceivable, such as: lack of motivation, inability to attend to relevant behaviour, or other factors inherent to the social context of imitation. It is also possible that the exact copying of an action requires an understanding of the model's intention to perform a certain act (Suddendorf & Whiten, 2001), thus making imitation a secondary representational or even metarepresentational achievement. The results presented in this chapter support this hypothesis in that no indications of recognising the imitator's intentions to imitate were found, suggesting that the monkeys did not employ secondary representations. However, the absence of testing behaviours in the presented experiments does not prove that monkeys are incapable of recognising intentional imitation; for example, this ability might emerge only after extended periods of being imitated. Hence, with more experience of being imitated, monkeys might show testing behaviours indicating intentional imitation recognition based on secondary representations.

An alternative hypothesis for why monkeys do not imitate is that monkeys may possess inadequate planning and inhibitory control skills to execute imitation. In comparisons with apes, monkeys show poor planning skills and low inhibitory control (e.g. in virtual maze tasks; Fragaszy, Johnson-Pynn, Hirsh & Brakke, 2003), which may be sufficient to hamper the production of imitation. However, recognising imitation does not rely on planning or inhibitory control of one's own motor behaviour, because the behaviour is executed before the cognitive match with the imitator's actions takes place. Hence if monkeys understand a model's intention behind a certain action but fail to imitate the action due to inadequate planning or inhibitory control, monkeys nonetheless might show recognition of the imitator's intentions in imitation recognition. The fact that no indications of intentional imitation recognition were observed suggests that inadequate planning and inhibitory control processes may not be the main hindrance to imitation by monkeys, but rather supports the hypothesis that imitative abilities hinge on an understanding of the model's intention for a certain act. Clearly, both hypotheses are calling out for more evidence.

Chapter summary

It has been hypothesised that imitation recognition may be achieved through primary representations (resulting in a visual preference) and secondary representations (resulting in contingency testing behaviours). In this chapter, two experiments are reported to test for imitation recognition in two monkey species. Pig-tailed macaques and capuchin monkeys were provided with an interesting object and faced by two experimenters: one imitating the monkeys' actions, and the other acting but not imitating. Results show that both pig-tailed macaques and capuchin monkeys visually discriminated between the two experimenters, however no instances of contingency testing were observed. These findings support the hypothesis that both species can use primary representations, but no evidence for any secondary representational abilities was obtained.

Chapter 4: A Mark Test Assessing Mirror Self-Recognition in Pig-Tailed Macaques

In Chapter 4, secondary representations in relation to mirror self-recognition (MSR) are investigated. MSR has been systematically studied in humans and animals for over 30 years, with mostly robust findings: some species quite consistently pass MSR tests, other species consistently fail. The basis for this dichotomy could potentially be a difference in secondary representational abilities. Below, the relationship between secondary representations and MSR is outlined, followed by a brief review of the MSR literature in humans, apes and other primates. A formal mark test is then reported using pig-tailed macaques, drawing on previous reports of MSR in pig-tailed macaques and the results of the experiments reported in the previous chapter. The discussion relates the findings of this mark test back to secondary representational abilities, and outlines potential future research.

4.1. Secondary representations and MSR

MSR can be regarded as a special form of imitation recognition with the crucial difference that the imitator happens to be oneself. As discussed in Chapter 3, imitation recognition requires the matching of kinaesthetic information (own movements) with the visual information originating from an imitator (imitator's movement) in order to recognise the contingency between the two. Matching both types of sensory information can be achieved through primary representations since it only requires a single updating model of reality to conceive of the match (i.e. mapping kinaesthetic to visual information). The same applies to recognising oneself in a mirror. Mirrors reflect objects accurately and faithfully, which means that movements of a mirror image are contingent (albeit reversed) to one's own movements. Hence, the first step to recognising oneself appears to be a kinaesthetic-visual match between one's own movements and the mirror image movements (Mitchell, 1993). However, in order to understand that the mirror image is not simply an object moving in synchrony with oneself, an individual has to realise that the mirror reflects objects, which is presumably based on the recognition of not only structural contingency but also the identical visual appearance of objects and mirror reflections. This recognition may prompt an understanding that the same object cannot be in two places at the same time (Perner, 1991), therefore the mirror is understood as a reflective surface. According to Perner (1991), this realisation requires the concurrent entertainment of multiple models of reality: primary representations of objects or oneself ("myself in reality") together with secondary representations of objects or oneself ("myself in the situation reflected in the mirror"; pp. 133). Two concurrent models of reality based on secondary representations may therefore be the basis of mirror self-recognition.

It is less clear, however, on what basis perceptions of mirror images become secondary representations rather than primary representations of reality. That is, what prompts an individual to conceive of its mirror image as a reflection of itself rather than an astonishingly accurate imitator? Mitchell (1993) put forward two theories to explain this necessary step for MSR. His inductive theory postulates that in order to recognise itself in the mirror, an individual must be capable of kinaesthetic-visual matching (a requirement also posed by imitation recognition) and in addition, realise that a mirror shows accurate and faithful reflections of reality. Mitchell (1993) argues that, by process of induction, an individual may reason that a) a mirror reflects reality and b) the mirror image moves when I move, therefore c) the mirror image must be my own reflection. Consequently, an understanding of mirrors and their properties may prompt MSR. Mitchell's (1993) second theory, his so-called deductive theory, argues along similar lines. According to the deductive theory, an individual must know that mirrors are accurate reflections of reality, and furthermore have an understanding of object permanence and perceive its own body parts as distinct objects yet continuous with the rest of its body (what Mitchell (1993) calls 'objectification'). These requirements may prompt MSR via a) an understanding that mirrors reflect reality, b) an understanding that the mirror image of one's own hand corresponds to the visual appearance of one's own hand, and c) inference based on object permanence and body part objectification that body parts which are not visually observable nonetheless correspond to body parts as seen in the mirror (because body parts are perceived as distinct yet also as a continuous whole).

Several criticisms have been made with regard to both theories (see Gallup & Povinelli, 1993; Anderson, 1993; De Lannoy, 1993; Byrne, 1993). For example, Gallup and Povinelli (1993) argued that both theories are equally deductive or inductive with regards to achieving MSR, thus Mitchell's terminology is deemed confusing at best and misleading at worst. Furthermore, the relationship between object permanence and MSR has been criticised as being merely correlational not causal (De Lannoy, 1993), and the combination of necessary steps within each theory has been described as somewhat arbitrary (Anderson, 1993). However, there appears to be general agreement that an understanding of mirrors as reflective surfaces is a necessary requirement for MSR. One important factor that underlies

MSR may be the strict temporal contingency that mirrors offer. Whilst human infants recognise themselves in a mirror at around 18-24 months of age (see below), if the temporal contingency is removed by using a delayed video play-back rather than a mirror children only pass self-recognition tests between 3-4 years of age (Povinelli, Landau & Perilloux, 1996). The criteria for passing tests of self-recognition are further outlined below.

4.2. MSR in human infants

MSR studies were pioneered by Gallup (1970) with chimpanzee subjects; however, Amsterdam (1972) independently developed similar tests for human infants. When exposed to a mirror, infants aged 12-15 months display a variety of behaviours suggestive of kinaesthetic-visual matching with the mirror image. For example, infants may direct smiles and vocalisations at the mirror image (Lewis & Brooks-Gunn, 1979). These behaviours point to a recognition of the contingency between self and mirror image and suggest social overtones rather than self-recognition (see also Chapter 3 for discussion on social responses and imitation recognition). To formally test if infants recognise themselves, the mirror is temporarily removed and a mark is unobtrusively applied to the infant's head (e.g. by wiping the infants' nose with a rouge-marked cloth) so that the infant remains ignorant of the mark's presence. If an infant recognises itself in the mirror, then after the re-introduction of the mirror the infant may notice the irregularity on its face and attempt to touch the mark. Crucially, if it recognises that the mirror image is a reflection of itself, it will touch the mark on it's own head; if it perceives the mirror image to be another infant, it may attempt to touch the mark on the infant's head in the mirror, or ignore the mark altogether. Human infants generally respond by touching their own head between 18-24 months of age (Amsterdam, 1972; Lewis & Brooks-Gunn, 1979), which is often referred to as having passed the mark test.

4.3. The mark test as a measure of 'self-hood'

At this point, a short note may be required with regards to the implications some researchers attribute to positive (passed) mark tests. Gallup (1977) argued that "the capacity to correctly infer the identity of the reflection must [...] presuppose an already existent identity on the part of the organism making that inference" (pp. 334). In other words, Gallup (1977) argues that positive mark tests may indicate a "sufficiently well-integrated self-concept" (pp. 334). If this concept implies an awareness of one's own thought processes and mental states, then passing the mark test would become synonymous with a metarepresentational achievement. However, at least in human infants, mark tests are passed long before other tasks indicative of metarepresentational abilities (such as TOM tests) are passed (18-24 months for MSR vs. 4.5 years for TOM). Furthermore, autistic children who generally fail TOM tasks can nonetheless pass standard mark tests (Dawson & McKissick, 1984), which suggests that the two abilities do not rely on the exact same mechanism. Therefore, rather than a measure of metarepresentational abilities, the mark test is perhaps better conservatively regarded as an indicator of the ability to recognise one's own body and appearance, which can be achieved through secondary representations (see above). Secondary representations may be sufficient to recognise one's own appearance in the mirror based on the perfect temporal and structural contingency of a mirror image (Perner, 1991), however secondary representations may limit the extent to which the affordances of both the mirror and one's own appearance are understood. In particular, secondary representations alone may not allow an individual to see the mirror image as a representation of oneself. Hence, metarepresentational abilities may be necessary to pass a delayed mark test (e.g. Povinelli et al., 1996) and to have an understanding of MSR beyond passing a mark test (see also Gergely, 1994).

Some researchers have criticised the mark test on methodological grounds as being an inadequate measure of self-recognition. In particular, Heyes (1994) argued that the mark test is not a suitable tool for comparative studies because of differences in species' ambient face touching, and claimed that positive findings for chimpanzees may be artefacts of anaesthesia (see also below for comparative MSR studies). Furthermore, species that fail mark tests may fail due to a variety of factors other than a lack of secondary representations. These shortcomings may include a lack of motivation to touch a mark, a failure to understand a mirror due to an avoidance of direct eye contact with the mirror image, or simply insufficient exposure to a mirror to learn about one's own appearance. A full discussion of these methodological issues is presented in Chapter 5.

4.4. MSR in apes

As already mentioned, Gallup (1970) pioneered the study of MSR with chimpanzees as subjects. Gallup exposed chimpanzees to mirrors for 10 days, and observed some interesting changes in behaviour. In the beginning, chimpanzees displayed to the mirror and treated the 'mirror chimpanzees' as if they were unfamiliar conspecifics. However, these social displays decreased over the first few days, and other behaviours emerged. For example, the chimpanzees engaged in contingency testing behaviours such as performing unusual or exaggerated gestures whilst visually monitoring themselves in the mirror. Furthermore, some individuals started to use the mirror to visually monitor themselves while grooming otherwise visually inaccessible areas of their bodies such as their faces, anal-genital regions or the tops of their heads. These behaviours were highly suggestive of mirror self-recognition to Gallup; the mark test was designed as a formal confirmation of MSR (Gallup & Povinelli, 1993).

Overall, Gallup's (1970) mark test is similar to Amsterdam's (1972) procedure used for human infants. The basic idea is the same: an individual is familiarised with mirrors and its own appearance in a mirror, a mark is applied to the individual's face without his/her knowledge, and responses to the mark are evaluated in the absence and presence of the mirror. If the mark is touched whilst the mirror is present but not when the mirror is absent, then the individual is deemed to have passed the mark test. Gallup's (1970) mark test shows some differences in methodology to the procedure for human infants. Unlike human infants, it may not be feasible to mark a chimpanzee's face without the chimpanzee noticing or indeed without presenting a serious risk to the human experimenter (although at least one study has applied marks unobtrusively by wiping young chimpanzees' faces several times before applying a mark, which is similar to the human infants' testing procedure; Lin, Bard & Anderson, 1992). Marks are therefore often applied while the animal is rendered unconscious using an anaesthetic. To avoid any confounding effects of the anaesthetic, animals are given enough time to fully recover before a mirror is re-introduced to them. Furthermore, primates are commonly marked on the forehead or the ears, which unlike the nose are guaranteed to be visually inaccessible without the use of the mirror. Primate studies are methodologically superior to human infant studies in this respect (Anderson & Gallup, 1999). MSR is also inferred if an animal shows spontaneous mirror-mediated self-directed responses (such as grooming otherwise visually inaccessible parts of the body with the aid of the mirror; Anderson, 1994).

Following the described procedures, at least some individuals of all great ape species have passed mark tests (see also Table 4.1). For example, chimpanzees (e.g. Gallup, 1970; Lethmate & Ducker, 1973; Suarez & Gallup, 1981) and orang-utans (e.g. Lethmate & Ducker, 1973; Miles, 1994) have both been reported to show mark directed responses. Bonobos appear to not have been subjected to a formal mark test yet, however a range of mirror-mediated self-directed responses have been observed (Walraven, van Elsacker & Verheyen, 1995). There are several studies failing to find evidence for MSR in gorillas (e.g. Suarez & Gallup, 1981; Ledbetter & Basen, 1982; Shillito, Gallup & Beck, 1999), with various theories of why gorillas may not readily pass mark tests (see Povinelli, 1994, for a discussion). However, at least two sign-using gorillas have passed a mark test (Patterson & Cohn, 1994). For the lesser apes, gibbons so far have failed mark tests (Lethmate & Ducker, 1973; Hyatt, 1998), despite showing mirror-mediated self-directed behaviours (Ujhelyi, Merker, Buk & Geissmann, 2000).

There are clear individual differences in the ability to self-recognise in a mirror within species. That is, in a self-recognising species such as the chimpanzee, some individuals repeatedly show evidence of MSR while others fail to show any evidence of MSR (however, some positive individuals fail to show evidence for

Table 4.1. Overview of MSR studies in nonhuman primates (adapted from Tomasello & Call, 1997). *number in brackets indicates number of positive animal

Study	**Species**	**Age of study animals**	**Number of subjects**	**Evidence for MSR?**
Gallup, 1970	Pan troglodytes	Juvenile	4	Yes (4)*
Lethmate & Duecker, 1973	Pan troglodytes	8-9 y	2	Yes (2)*
Suarez & Gallup, 1981	Pan troglodytes	9-21 y	4	Yes (3)*
Povinelli et al., 1993	Pan troglodytes	1-16+ y	105	Yes (31)*
De Veer et al., 2003	Pan troglodytes	16-23 y	12	Yes (8)*
Lethmate & Duecker, 1973	Pongo Pygmaeus	Sub-adult	2	Yes (2)*
Miles, 1994	Pongo Pygmaeus	Juvenile	1	Yes (1)*
Walraven et al., 1995	Pongo Pygmaeus	2-23 y	7	Yes (5)*
Suarez & Gallup, 1981	Gorilla gorilla	13-19 y	4	No
Ledbetter & Basen, 1982	Gorilla gorilla	10-11 y	2	No
Patterson & Cohen, 1994	Gorilla gorilla	18-19 y	2	Yes (2)*
Lethmate & Duecker, 1973	Hylobates	Adult	2	No
Hyatt, 1998	Hylobates	Juvenile and Adult	10	No
Ujhelyi et al., 2000	Hylobates	7-22 y	3	Yes (2)*
Anderson, 1983	Macaca arctoides	Infant	10	No
Gallup, 1977	Macaca fascicularis	Juvenile	1	No
Mitchell & Anderson, 1993	Macaca fascicularis	12 y	1	No
Itakura, 1987	Macaca fuscata	5-6 y	2	Ambiguous (1)*
Gallup et al., 1980	Macaca mulatta	Infant and Adult	4	No
Lethmate & Duecker, 1973	Mandrillus sphinx	Adult	1	No
Lethmate & Duecker, 1973	Papio	Adult	1	No
Lethmate & Duecker, 1973	Cebus apella	Adult	1	No
Marchal & Anderson, 1993	Cebus apella	Juvenile and Adult	8	No
Riviello, Visalberghi & Blasetti, 1992	Cebus apella	Juvenile and Adult	4	No
Anderson & Roeder, 1989	Cebus apella	1-19 y	7	No
De Waal, Dindo, Freeman & Hall, 2005	Cebus apella	1-30 y	14	No
Hauser et al., 1996	Saguinus oedipus	Juvenile and Adult	6	Ambiguous (5)*
Hauser et al., 2001	Saguinus oedipus	Adult	16	No
Thompson & Boatright-Horowitz, 1994	Macaca nemestrina	9-18 y	3	Ambiguous (2)*
Boccia, 1994	Macaca nemestrina	Sub-adult and Adult	15	Ambiguous (1)*

MSR in subsequent mark tests; see de Veer et al., 2003). Furthermore, there appears to be a developmental trend in the ability to self-recognise in a mirror, at least in chimpanzees. Povinelli et al. (1993) tested a large sample of chimpanzees (n=105) for signs of MSR, and found that most animals that showed MSR fell within the adolescent/young adult age group. Povinelli et al. (1993) suggested that MSR emerges between 4.5-8 years, and may decline in older age (see also de Veer et al., 2003, for a replication of these results using the same animals). Others found evidence for MSR in much younger chimpanzees, for example Lin et al. (1992) reported positive mark tests for a chimpanzee aged 2 years and 4 months. While the exact age at which MSR can be found in chimpanzees remains unclear, the idea that MSR is a developmental achievement which emerges as an individual matures appears uncontroversial and is supported by evidence from both human infants and chimpanzees.

4.5. MSR in monkeys?

Numerous monkey species have been subjected to mirror studies or formal mark tests, including stumptailed macaques (Anderson, 1983; Gallup, 1970), longtailed macaques (Gallup, 1970; Gallup, 1977; Mitchell & Anderson, 1993), Japanese macaques (Itakura, 1987), rhesus macaques (Gallup, 1970; Gallup et al., 1980), mandrills (Lethmate & Ducker, 1973), olive and hamadryas baboons (Lethmate & Ducker, 1973) and capuchin monkeys (Lethmate & Ducker, 1973; see also Table 4.1). The results of these studies are largely unequivocal: monkeys do not pass mark tests. Cotton-top tamarins appeared to have passed an alternative mark test in one study (Hauser, Kralik, Botto-Mahan, Garrett & Oser, 1995), however some methodological aspects were criticised (Anderson & Gallup, 1997), and an attempted replication of the results failed (Hauser, Miller, Liu & Gupta, 2001).

Instead of touching the mark, monkeys generally persist in directing social responses at their mirror image. Although these social responses tend to wane with time, no reports of mirror-mediated self-directed responses are found in the literature (Anderson, 1994). Nonetheless, monkeys can use a mirror to find otherwise hidden food. For example, after seeing a hidden food reward in a mirror, macaques accurately approach the correct location and retrieve the food (Anderson, 1986). This type of behaviour does not necessarily suggest that the monkeys recognised the food reward in the mirror to be the exact same food reward that they retrieved, which would indicate secondary representational abilities. Instead, the monkeys may have perceived the food in the mirror to be a discriminative marker indicating the presence of food (which can be achieved using primary representations). This idea is supported by a study by Menzel, Savage-Rumbaugh & Lawson (1985), which used video equipment to present a hidden food reward to rhesus macaques. Menzel et al. (1985) report that the monkeys often threatened the video image of their own hand when it approached the food location, apparently not realising that it was their own hand. Chimpanzees on the other hand never showed social responses in response to their own hands, and completed the task successfully (Menzel et al., 1985). Together these studies suggest that monkeys, in contrast to apes, may be lacking the necessary secondary representational abilities to support MSR.

4.6. A mark test in pig-tailed macaques

Even though monkeys generally appear to fail mark tests, there are some reports of monkeys reacting to marks on their heads after seeing themselves in a mirror. For example, Itakura (1987) reports that one Japanese macaque touched a mark under his nose three times in the presence of a mirror. However, as the touching does not appear to have been accompanied by close visual monitoring of the gesture, Itakura (1987) argues that the reported mark-directed behaviours are not conclusive evidence of MSR in a Japanese macaque. Two further studies report positive mark tests for pig-tailed macaques. Thompson & Boatright-Horowitz (1994) reinforced three adult pig-tailed macaques for looking at their own mirror images. A subsequent mark test revealed that one monkey touched a mark on her brow with a knuckle, rubbed the mark, and subsequently inspected the knuckle. Another monkey is reported to have wiped a marked brow after looking into the mirror. Neither case is comparable to the close visual inspection of marks seen in great apes. Boccia (1994) also reports a positive mark test in pig-tailed macaques. Out of 15 monkeys tested, one adult female swiped her hand across the marked area on her head and subsequently inspected her own hand. This behaviour was repeated 4 times in the presence of a mirror, but not in the absence of a mirror. Furthermore, the same female grabbed the top of a marked ear immediately after looking at herself in the mirror. Hence, at least three pig-tailed macaques have been claimed to show some evidence supportive of MSR, which challenges the general agreement that monkeys cannot recognise themselves in a mirror.

Perhaps pig-tailed macaques are an exception to the rule? As reported in Chapter 3, pig-tailed macaques distinguish between an imitator and a non-imitator of their own actions, quite possibly on the basis of kinaesthetic-visual matching (see Chapter 3 for further details) which is thought to be a necessary requirement for MSR (Mitchell, 1993). The fact that the monkeys did not engage in contingency testing behaviours during the imitation recognition study (sudden unexpected movements whilst visually monitoring the experimenters as if to introduce deliberate non-contingency), which are thought to be a clear indicator of secondary representational abilities, does not necessarily imply that they lack secondary representations, not the least because absence of evidence does not entail evidence of absence (Desmond, 1979). Based on these considerations four pig-tailed macaques were selected from the previous imitation recognition experiment: two monkeys that showed a clear preference for the imitator in the imitation recognition study, and two monkeys that showed the least preference for the imitator. If kinaesthetic-visual matching abilities are a necessary requirement for MSR, then a visual preference for an imitator might be expected to correlate with evidence for MSR. In the following experiment, all four monkeys were familiarised with their own mirror images, and subsequently subjected to a formal mark test.

4.6.1. Subjects

The same subjects that were tested for the imitation recognition study (Chapter 3) were considered for this MSR study. Two individuals with a high preference for the imitator and two individuals with a low preference for the imitator in the previous experiment were chosen on the basis of their other experimental commitments. The two monkeys with low preferences were Charlie (male, 4 years) and Alcatraz (male, 18 years); the two monkeys with high preferences were Sofia (female, 7 years) and David (male, 6 years). Charlie, Alcatraz and David had also previously participated in the self-imitation study reported in Chapter 2. For further details on housing, see Chapter 3.

4.6.2. Procedure

All monkeys were individually tested in their home cages. Each monkey received daily mirror exposure sessions during which a large glass mirror (50 x 60 cm) was placed ca. 60 cm in front of the monkeys' home cages. A video camera placed above the mirror recorded the first 10 minutes of each session. Mirrors remained in front of the home cages between one and four hours every day, depending on other routine procedures being carried out in the laboratory. Charlie and Sofia both received 10 sessions of mirror exposure (total of 30.5h and 30h exposure respectively); Alcatraz received 11 sessions (total of 37.5h exposure), and David received 13 sessions (total of 40h exposure). The monkeys were not food deprived for this experiment, and were given their normal food rations after the first 10 minutes of mirror exposure. Water was available ad libitum.

The mark test was carried out the day after the last mirror exposure session of each monkey. Charlie, Alcatraz and David were anaesthetised with 0.3ml, 0.8ml and 0.4ml ketamine (*Ketaret 50*, 5g/100ml, Farmacentici Gellini) respectively, which caused severe drowsiness and reduced motor control but not complete unconsciousness. The monkeys were then restricted in their home cages to reduce the risk of injury, and red marks (ca. 1cm in diameter) were applied to their left inside wrist, left eyebrow ridge and top of the right ear using a waterproof marker pen (see Figure 4.1 for an example). The monkeys did not respond to the marks or the experimenters at this point. The marks on the wrists served as controls to verify the monkeys' interest in red marks on their bodies (Gallup et al., 1980); only responses to the marks on the faces were taken as evidence of MSR. To test the mark's olfactory and tactile properties, the experimenter applied marks to her own

Figure 4.1. Example of eyebrow, ear and wrist marks on Alcatraz (top) and Charlie (bottom).

wrist and forehead. A faint chemical odour was initially noticeable but became imperceptible after ca. 5 minutes. No tactile feedback was detected, which made this type of mark suitable for the current experiment. The monkeys were given time to recover from the anaesthetic, and ca. 2 hours later were fully released when judged to have regained complete motor control.

The fourth monkey, Sofia, had undergone surgical procedures 2 years previously, and had been implanted with head restraint implants and a neuronal recording chamber at the top right side of her head. She had fully recovered and did not show any behavioural abnormalities from this procedure, and was thus considered suitable for the present experiment. Sofia regularly participated in single neuron recording studies, but not during the course of this experiment. The marks were applied during routine procedures to clean the neuronal recording chamber while Sofia was sitting in a primate chair with her head and neck restrained and arms free for movement. Sofia did not attempt to touch the marks during or just after their application. After the marks were applied, Sofia was returned to her home cage.

After the monkeys were released into their home cages with marks applied to wrist, eyebrow ridge and ear, the mirror was placed ca. 60 cm in front of the home cages with the non-reflective side facing the monkeys. Any mark-directed responses, such as scratching, grooming, or touching the marked areas, were recorded in real time by the experimenter. In addition, any responses to the mark-opposite body areas (unmarked wrist, unmarked eyebrow ridge, unmarked ear) were recorded as controls (Povinelli, Gallup, Eddy & Bierschwale, 1997). After 30 minutes of observations the monkeys were given their normal food rations, and were given a further 2 hours for recovery.

In the final phase of the experiment, the monkeys were confronted with their mirror images. The mirror was turned around so that the reflective side faced the monkeys, and the monkeys were filmed for 30 minutes with a video camera placed above the mirror. All responses towards the marked areas as well as responses to the mark-opposite areas were recorded by the experimenter in real time.

4.7. Results

The amount of time spent looking at the mirror and social responses directed at the mirror during the first 10 minutes of the mirror exposure sessions and during the first 10 minutes of the mark test for both the mirror and control phase were scored from the video tapes (25 frames/second) for each monkey. In addition, mark and opposite-mark directed responses during test sessions were verified from the tapes, and any possible instances of contingency testing (sudden, unexpected movements whilst visually monitoring themselves in the mirror) and mirror-mediated self-directed responses were noted.

4.7.1. Exposure sessions

Figure 4.2 shows the amount of time the monkeys spent looking at the mirror during mirror exposure sessions and the mark test. It should be noted that the mirror was positioned so that the monkeys could not only see themselves in the mirror, but also the monkeys in the cages adjacent to their own cage. The monkeys frequently used the mirror to look at their neighbours in this way, however as it was not always clear whether they looked at themselves or at the other monkeys, all instances of looking at the mirror were coded and are presented below. Visual attention towards the mirror significantly decreased across exposure sessions ($r=-0.912$, $p<0.001$). Using Grubb's Test for detecting outliers, visual attention during the mark test did not differ significantly from the amount of time spent looking at the mirror during the last 4 exposure session for Sofia, Alcatraz and Charlie ($p>0.05$); however, David looked significantly longer at his own reflection during the mark test (Grubb's test: $z=1.74$, $p<0.05$).

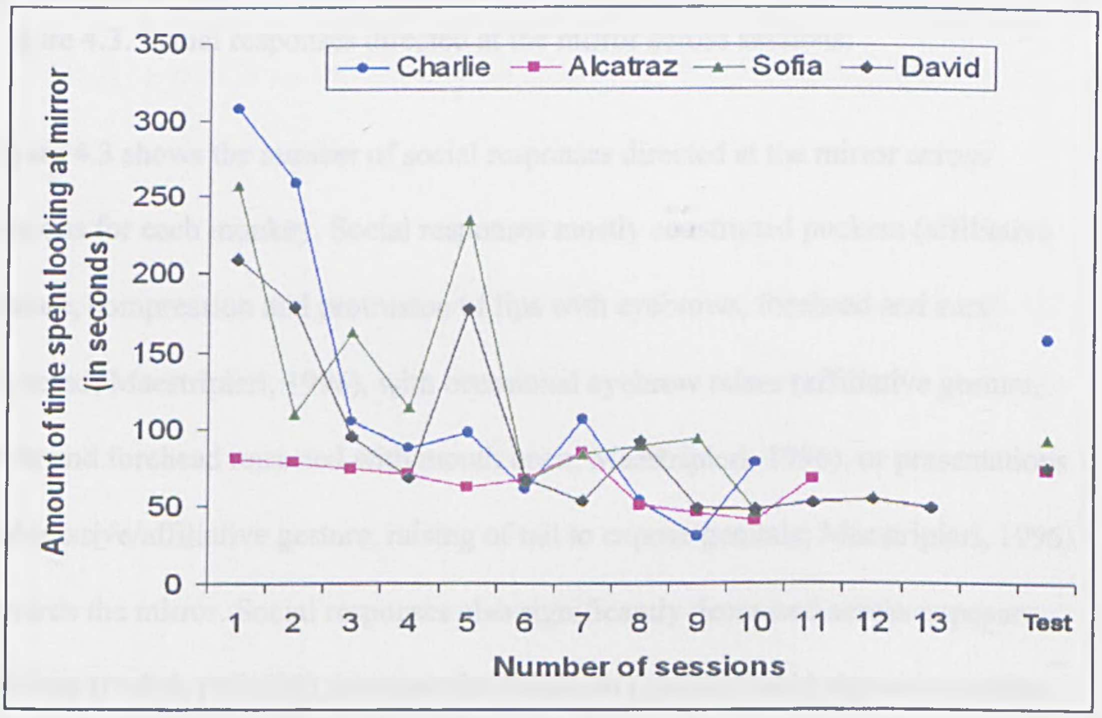

Figure 4.2. Amount of time spent looking at the mirror across sessions.

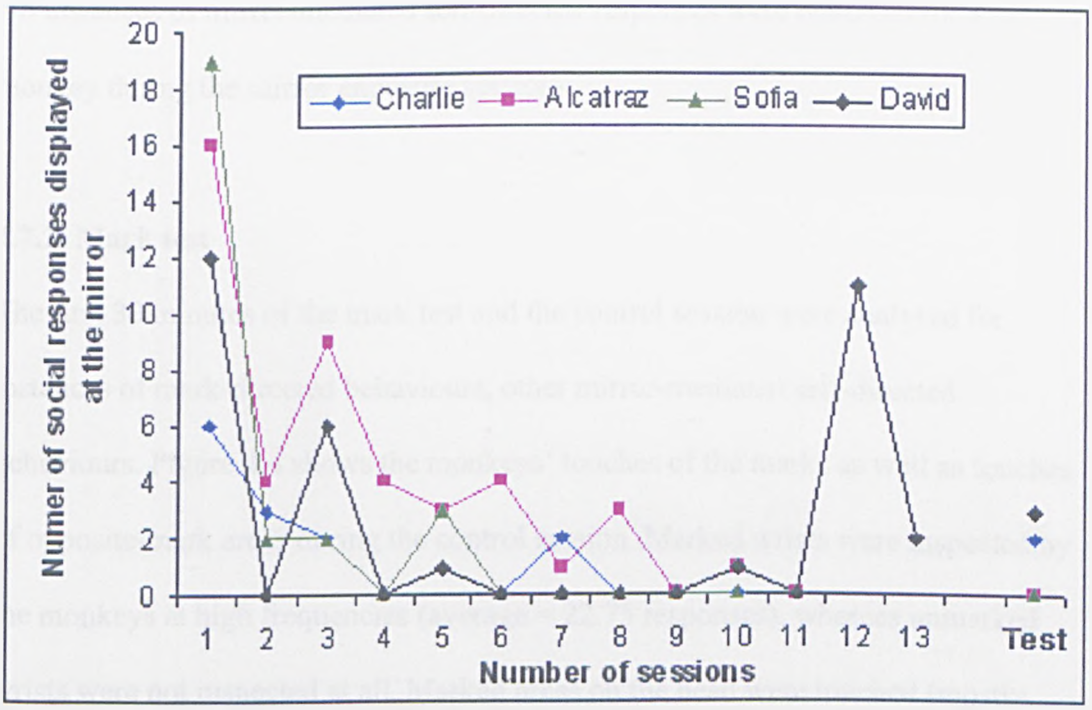

Figure 4.3. Social responses directed at the mirror across sessions.

Figure 4.3 shows the number of social responses directed at the mirror across sessions for each monkey. Social responses mostly constituted puckers (affiliative gesture, compression and protrusion of lips with eyebrows, forehead and ears retracted; Maestripieri, 1996), with occasional eyebrow raises (affiliative gesture, brow and forehead retracted with mouth open; Maestripieri, 1996), or presentations (submissive/affiliative gesture, raising of tail to expose genitals; Maestripieri, 1996), towards the mirror. Social responses also significantly decreased across exposure sessions (r=-0.6, p=0.039), however for unknown reasons David showed a sudden increase in social responses in his second last exposure session. The number of social responses directed at the mirror during the mark test did not differ significantly from the mean number of social responses directed at the mirror during the last 4 exposure sessions (binomial tests: all p>0.05).

No instances of mirror-mediated self-directed responses were observed for any monkey during the mirror exposure sessions.

4.7.2. Mark test

The first 30 minutes of the mark test and the control session were analysed for instances of mark-directed behaviours, other mirror-mediated self-directed behaviours. Figure 4.4 shows the monkeys' touches of the marks as well as touches of opposite-mark areas during the control session. Marked wrists were inspected by the monkeys at high frequencies (average = 22.75 responses), whereas unmarked wrists were not inspected at all. Marked areas on the head were touched (mostly scratched) no more frequently than other areas on the head (both averages = 2.25 responses).

Figure 4.5 shows the monkeys' touches of the marks as well as touches of opposite-mark areas with the mirror present. The marked wrists now elicited fewer responses (average = 2 responses), and unmarked wrists as well as unmarked head areas were not touched at all. Sofia scratched the mark on her eyebrow ridge once; David rubbed his marked ear 8 times, and scratched his marked ear once. Neither monkey visually monitored the contact with the marks via the mirror during any mark-directed response, nor did they inspect their hands after touching the mark. No instances of other mirror-mediated mark directed responses were observed for any monkey during the mark test.

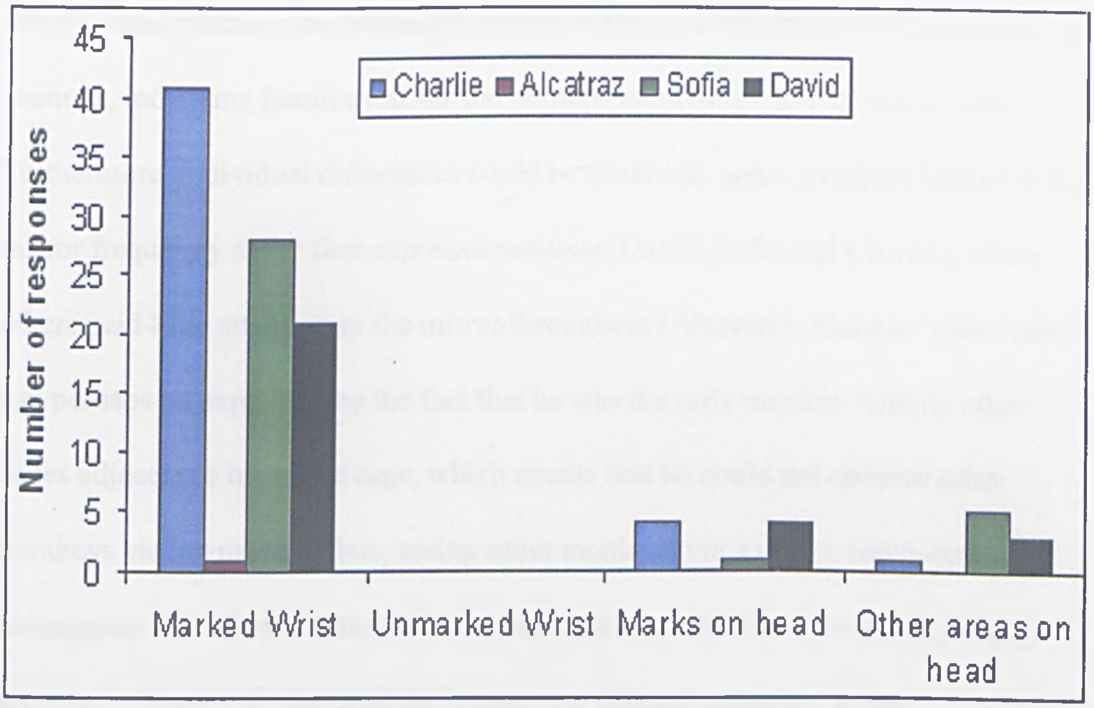

Figure 4.4. Touching responses to marked and opposite-mark areas without mirror

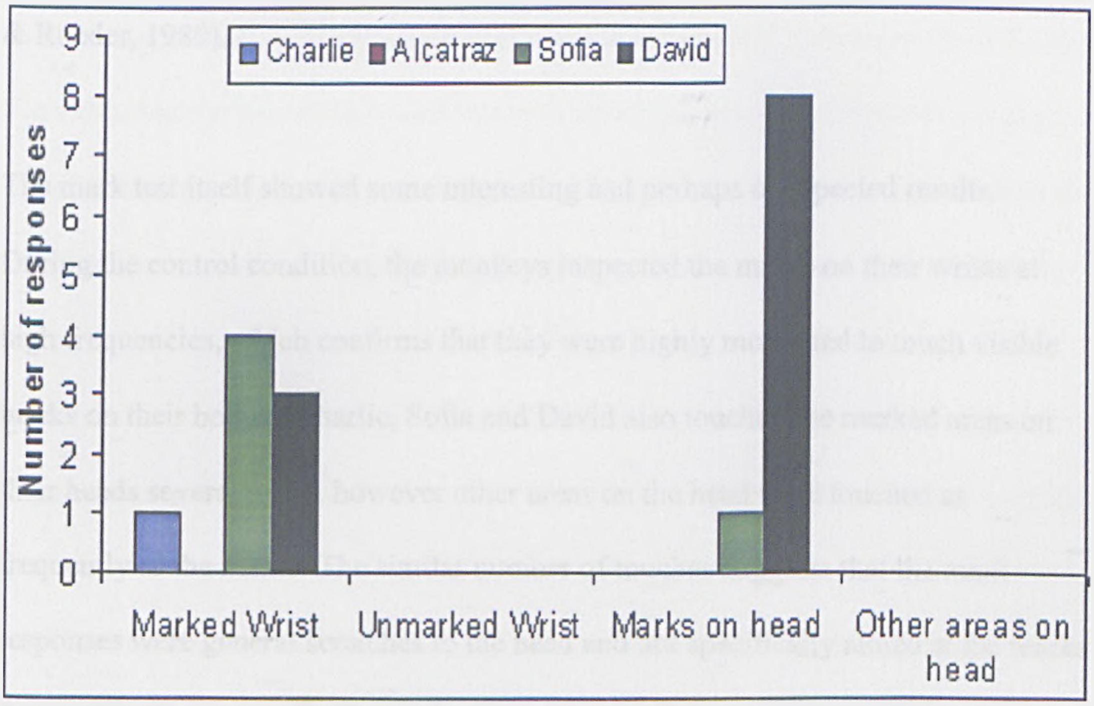

Figure 4.5. Touching responses to marked and opposite-mark areas with mirror

4.8. Discussion and Conclusion: The mark test in pig-tailed macaques

The presented experiment confirmed many previous findings of MSR studies in monkeys. For example, common with other studies (e.g. Anderson & Roeder, 1989), visual attention and social responses to the mirror decreased over exposure sessions, indicating familiarisation and perhaps habituation to the mirror image. Furthermore, individual differences could be observed: some monkeys looked at the mirror frequently at the first exposure sessions (David, Sofia and Charlie), while others paid little attention to the mirror throughout (Alcatraz). Alcatraz' disinterest can perhaps be explained by the fact that he was the only monkey with no other cages adjacent to his home cage, which means that he could not observe other monkeys via the mirror. Thus, seeing other monkeys via a mirror can potentially enhance an individual's interest and understanding in his/her own mirror image, although efforts to facilitate MSR in monkeys through paired or group exposure to mirrors have consistently failed (e.g. Gallup et al., 1980; Anderson, 1983; Anderson & Roeder, 1989).

The mark test itself showed some interesting and perhaps unexpected results. During the control condition, the monkeys inspected the marks on their wrists at high frequencies, which confirms that they were highly motivated to touch visible marks on their bodies. Charlie, Sofia and David also touched the marked areas on their heads several times, however other areas on the head were touched as frequently as the marks. The similar number of touches suggests that the mark responses were general scratches to the head and not specifically aimed at the marks due to olfactory or tactile discomfort, which would have invalidated the mark test (because the monkeys would have been aware of the mark without seeing themselves in the mirror first). When the mirror was re-introduced, both David looked significantly longer at the mirror when compared to previous exposure sessions. Even though monkeys may habituate to their own mirror image and a resurgence of social responses and visual attention may occur following alterations to the animals' visual appearance or the mirror's location, an increase in visual attention in itself does not necessarily indicate that a monkey recognises itself (Anderson, 1994). Rather, increases in attention potentially indicate that David noticed the change in appearance without necessarily implying that he recognised that it was his own mirror reflection which had changed.

Far more telling are self-directed responses to the mark following re-introduction of the mirror. Similar to a small number of individuals in previous studies with pig-tailed macaques (Boccia, 1994; Thompson & Boarright-Horowitz, 1994), both Sofia and David touched the mark during the mark test. Neither of them touched other areas on their heads. Sofia scratched her marked ear once. However, as the response was neither preceded nor followed by close visual monitoring of her mirror image, it cannot be regarded as strong evidence for MSR. Similarly, David showed several responses to his marked ear and no responses to other areas on his head. However, David frequently performed these rubs and scratches to his ears independently of the experimental or other context (personal observation), and they might indicate stereotypies caused by socially and environmentally suboptimal housing, or perhaps an undiagnosed medical condition of his ears. Since David's responses failed to be accompanied by any visual monitoring via the mirror, they also should not be regarded as conclusive evidence of MSR.

In addition to mark-directed responses, the monkeys were also observed for other mirror-mediated self-directed responses whilst exposed to the mirror. None were found in any monkey, which confirms the lack of evidence for MSR. However, it is noteworthy that David and Sofia, the monkeys who apparently responded to the mark, were also the two monkeys that showed the strongest visual preference for the imitator in the imitation recognition experiment. Thus it remains an intriguing hypothesis that an ability to engage in kinaesthetic-visual matching may facilitate or prompt MSR, however the evidence from the presented experiment is not strong enough to decisively draw any further conclusions on this issue.

4.9. Future research potential

The results of this experiment cannot be seen as evidence for MSR in pig-tailed macaques, which confirms previous findings on the probable absence of secondary representational abilities in this species (see Chapter 3). However, the somewhat ambiguous result in this experiment together with previous reports of mark-directed responses during mark tests in pig-tailed macaques (Boccia, 1994; Thompson & Boatright-Horowitz, 1994), certainly point to further research potential regarding MSR in this species. One line of research that has received little subsequent attention in the literature is macaques' ability to use the mirror to find otherwise hidden food items. Even though it is known that macaques can use mirrors in this way (Anderson, 1986), it is far less clear what the monkeys understand about mirrors in this context. That is, do monkeys understand that the reward in the mirror is the same reward that they will receive? Do they use the image of their own hand to guide their movement, or does the reflected food merely serve as a discriminative marker? Can monkeys distinguish between the image of their own hands and the image of a conspecific's hand approaching the food? Furthermore, Thompson & Boatwright-Horowitz (1994) pointed out that valid competence in mirror use also requires "instrumental behaviour maintained by bringing the mirror or the self into appropriate positions for [mirror-mediated locating and reaching]" (pp. 336), that is, competence to position the mirror functionally to oneself. So far, this aspect of mirror competence does not appear to have been investigated in monkeys, but it would further clarify monkeys' understanding of mirrors and their use (see also Chapter 5). In addition, further advances in video technology make it feasible to test the effects of structural and temporal displacements of monkeys' mirror/video-mediated behaviours, which might help to clarify monkeys' limitations of their understanding of mirrors. These lines of research would provide valid alternatives to the mark test to investigate secondary representational abilities in monkeys, and given the results described here and elsewhere, pig-tailed macaques may be a promising monkey species for these investigations.

Chapter Summary

Pig-tailed macaques were shown capable of kinaesthetic-visual matching in the previous chapter, which is also thought to be a necessary requirement for mirror self-recognition (MSR). In addition two reports of potentially positive mark tests in this species can be found in the literature, which suggests that pig-tailed macaques may be capable of MSR. A formal mark test was carried out with 4 monkeys from the previous experiment, using two who showed a strong preference and two who showed a weak preference for the imitator. Results reveal that the two monkeys with the strong preference for the imitator contacted the marks on their heads during the mirror exposure phase. Even though the results cannot be judged to be strong evidence for MSR, they suggest a relation between kinaesthetic-visual matching abilities and MSR.

Chapter 5: A Mirror Study with Capuchin Monkeys

The previous chapter reported a mark test with pig-tailed macaques, drawing on evidence of kinaesthetic-visual matching (see Chapter 3) and previous mark tests suggestive of mirror self-recognition (MSR) in this species. The reported mark test can only be judged to be ambiguous at best, however failure to show clear evidence of MSR may be due to a variety of shortcomings other than a lack of secondary representational abilities. This chapter outlines some of the criticisms that have been made with regard to methodological issues surrounding MSR and some manipulations that have attempted to address these shortcomings and prompt MSR in monkeys. A new manipulation is presented using capuchin monkeys as subjects, which is hypothesised to increase monkeys' understanding of mirrors through increased manipulatory access and confrontation with two mirror surfaces, which together may facilitate behaviours indicative of MSR. The discussion considers implications for MSR in capuchin monkeys and the value of mirrors in psychological research with nonhuman primates.

5.1. Heyes' (1994) critique of the mark test in nonhuman animals

Chapter 4 outlined the rationale and methodology of Gallup's (1970) mark test, and cited evidence that, similar to human infants, chimpanzees and orang-utans have convincingly shown signs of MSR whereas the evidence for gorillas was initially disputed but has gradually been accepted (see Chapter 4 for a detailed discussion). However, a literature review by Heyes (1994) outlined some reservations regarding the methodological aspects of animal MSR studies, and claimed that MSR had not been conclusively demonstrated in animals. Heyes pointed out that a potential confound for mark tests in animals is the sequence in which the mark test is administered. First, the test animal is anaesthetised to apply the facial marks, followed by a control observation period, and finally the mirror is re-introduced. Heyes argued that this fixed sequence of events may have introduced an experimental bias into mark tests because the control observation period could potentially be influenced by lingering effects of the anaesthesia. Specifically, Heyes claimed that after-effects of the anaesthetic could potentially depress self-directed responses during the control observation period but not during the subsequent mirror exposure period. Thus, what is interpreted as mirror-mediated self-directed behaviours may in fact be no more than self-directed behaviours that normally occur frequently but that are suppressed during the control period. Heyes argued that the mark test cannot be seen as a suitable comparative tool because of species-specific differences in ambient face touching. That is, some species are more likely than others to groom parts of their own face or head, and therefore these species may more readily pass mark tests than those who do not engage in these behaviours on a regular basis.

Both of Heyes' (1994) points are valid theoretically – the fixed sequence of the mark test and species-specific differences in face touching could potentially bias results. However, as Gallup et al. (1995) showed, neither objection applies in practice. Regarding the effects of anaesthesia, several animal studies have conducted mark tests without the use of an anaesthetic e.g. Patterson & Cohen (1994), Lin et al. (1993) and Miles (1994). The result, however, remained the same: chimpanzees, an orang-utan and a gorilla showed distinct mark-directed responses during the mirror exposure period but not the preceding control period. These results cannot be explained by suppressed facial touching due to the effects of anaesthetics, but suggest self-directed behaviours in response to viewing themselves in the mirror. Furthermore, Gallup et al. (1995) presented data to show that chimpanzees make self-directed responses distinctively to the marked areas and not the unmarked areas of their heads, which would not be expected if face touching occurred as a general response and not specifically to seeing the mark in the mirror (see also Povinelli et al., 1997). Gallup et al. (1980) also pointed out that previous reports on low levels of face touching in monkeys might have been confounded by a variety of computational and statistical errors, and a subsequent study of face touching showed similar levels of face touching for chimpanzees and macaques (Suarez & Gallup, 1986). Therefore the two methodological factors outlined by Heyes (1994) appear to contribute little if any to apes' ability to pass and monkeys' failure to pass mark tests; they do, however, point to the importance of addressing potential methodological confounds in MSR studies.

5.2. Negative mark tests and secondary representations

Chapter 4 also argued that passing a mark test can be seen as evidence for secondary representational abilities, and according to Mitchell's (1993) theories on MSR, also as evidence for kinaesthetic-visual matching and an understanding of mirrors as reflective surfaces, or object permanence and 'body part objectification'. However, a negative mark test is difficult to interpret in that not only can a lack of secondary representations explain the outcome, but also insufficiencies in one or more of these supporting factors. It seems reasonable to assume that an individual capable of secondary representations is unlikely to recognise himself/herself in a mirror if he/she has never seen a mirror before and therefore does not understand the reflective properties of mirrors. Given that monkeys appear to consistently fail MSR tasks, researchers speculated that perhaps monkeys are limited in these other cognitive domains, and have therefore devised a variety of interventions attempted to address this issue.

5.3. Potential shortcomings preventing MSR in monkeys

Potential shortcomings that might prevent MSR and have been addressed experimentally in the literature broadly fall into two categories: failure to understand mirrors as reflective surfaces and insufficient motivation to touch marks. The rationale behind both shortcomings and the outcomes of experimental manipulations are discussed below (see also Anderson & Gallup, 1999).

5.3.1. Failure to understand mirrors as reflective surfaces

As mentioned above, individuals who fail to understand that a mirror accurately reflects environmental information conceivably could not understand that their own mirror reflection is identical to their own physical appearance. Therefore, a failure to understand mirrors could potentially prevent MSR even in the presence of secondary representational abilities. Numerous attempts have been made to increase monkeys' understanding of mirrors by e.g. giving them extended mirror exposure from birth or shortly thereafter (Gallup et al., 1980; Anderson, 1983), and sometimes even for several years (Gallup, 1994); by increasing physical access to mirrors (Anderson & Roeder, 1989; Anderson, 1983); by providing access to mirrors within a social group so that an individual can see others both in reality and in the mirror (Gallup et al., 1980; Anderson, 1983; Anderson & Roeder, 1989) or by reinforcing mirror-mediated responding (Anderson, 1984; Anderson, 1986). None of these factors prompted behaviours indicative of MSR in monkeys. Another potential confounding factor is the direct eye contact with a mirror image, which in many monkey species (but not in apes) may be perceived as a threat gesture and therefore result in avoidance of the own mirror image (Anderson & Roeder, 1990). Consequently, monkeys may be less prone to learn about their own mirror images than apes. Presenting mirrors at an angle so that direct eye contact is prevented failed to show any signs of MSR in capuchin monkeys (Anderson & Roeder, 1990), however similar manipulations also failed to induce mark-directed behaviours in two gorillas (Shillito et al., 1999). On the other hand, reinforcing macaques for direct eye contact with their own mirror images led to ambiguous mark test results in pig-tailed macaques (Thompson & Boatright-Horowitz, 1994; but see discussion on the potential exception of pig-tailed macaques and MSR in Chapter 4).

5.3.2. Insufficient motivation to touch marks

A second potential confounding factor concerns an individual's motivation to investigate marks on its body. Conceivably, an individual may recognise itself in a mirror and see a mark on its forehead, yet if it is not motivated to touch the mark, then it will fail the mark test despite being able to recognise itself. To ensure that monkeys are motivated to touch marks on their bodies, some studies reinforced touches to marks on other parts of the body (Thompson & Boatright-Horowitz, 1994), used sequential marks on different body parts (Anderson, 1984), attempted to train touches to the head (Anderson, 1984) or increased the mark's saliency (Benhar et al., 1975); no manipulation led to conclusive evidence of MSR. Hauser et al. (1995) took a rather drastic approach to increase the mark's salience for cotton-top tamarins by dying their distinct white tufts of hair on top of their heads brightly green, pink or purple colours. Hauser et al. (1995) reported several touches to the dyed hair tuft in several monkeys, and interpreted these results as showing MSR. However, as Anderson & Gallup (1997) point out, Hauser et al. (1995) failed to include a control period, and other behaviours indicative of MSR (such as mirror-mediated self-directed responses) were not observed, which questions this (unexpected) positive result. Indeed, a better controlled replication attempt failed to yield similar results (Hauser et al., 2001). Marks on body parts that are directly visible to monkeys, however, are investigated readily and in detail (e.g. Gallup et al., 1995) which suggests that a lack of motivation to touch marks on their bodies is an unlikely cause that prevents monkeys from passing a mark test.

5.4. A new manipulation: Increased access and exposure

Given that it remains possible that monkeys possess secondary representational abilities yet fail MSR studies due to other cognitive limitations, a failure to understand mirror properties appears to be a more likely cause of failed MSR studies than a lack of motivation to touch marks on head areas. Here, a new manipulation was attempted aimed at increasing mirror understanding in a monkey species. It was based on the finding that although rhesus macaques may habituate to a mirror and cease showing social responses towards it, when the mirror is moved to a different location social responses may return (Suarez & Gallup, 1986). Therefore stationary mirrors in one particular place may lead to associations between mirror images and that particular location, yet prevent a more generalised understanding of mirrors. In the present experiment, monkeys were simultaneously exposed to one large fixed mirror outside the test cage and one smaller portable mirror within the test cage. It was hypothesised that two mirrors might increase the monkeys' understanding of mirrors by seeing their reflections at two different places simultaneously. In particular, rather than associating their mirror images with one specific mirror in a certain location, the monkeys might come to understand mirror properties and reflections in general, which in turn could prompt self-recognition as indicated through mirror-mediated self-directed behaviours (for example, grooming otherwise visually inaccessible body parts with the aid of the mirror).

Two additional considerations were taken into account for the experimental design. Different types of small mirror objects were presented to the monkeys in order to reduce habituation and maintain the monkeys' interest in the mirrors, and to test the effects of various physical properties of the mirror on the monkeys' interest in the mirrors and subsequent MSR behaviours. Hall (1962) presented various reflective objects to patas monkeys, and reported "clear evidence for differential stimulating effects according to the degree of mirror-image discernible" (pp. 1259). However, exactly what these effects were was not reported in detail. The present study therefore investigated the effect of discernible mirror-images in detail and also the effects of physical alterations to the mirror shape, which might impact on monkeys' mirror experiences. Hall (1962) also reported that the monkeys engaged in 'oblique looks', e.g. looking closely into a mirror at an angle and turning to check the real environment (also Anderson & Roeder, 1989). These 'oblique looks' appear to be a suitable measure of basic mirror understanding, and the present study aimed to investigate the effects of different mirror properties on this type of behaviour. Furthermore, two mirrors give monkeys the unique opportunity to manipulate mirrors in order to see body parts not even visible with one mirror (e.g. the back of their head). Such manipulatory behaviour would be the first evidence of instrumental behaviour involving the positioning of mirrors by nonhuman animals, and could be seen as evidence for competent mirror use (see Thompson & Boatright-Horowitz, 1994).

The outlined manipulations were conducted with capuchin monkeys (*Cebus apella*) as subjects. As already mentioned in Chapter 1, capuchin monkeys are notable for their advanced cognitive abilities, manifested through their flexible tool use (Beck, 1980; Fragaszy & Adams-Curtis, 1991, Visalberghi, 1990), and presumably a consequence of their relatively large brain size (Gibson, 1986), which may make them more likely to show signs of MSR than other monkey species. Capuchin monkeys have already been subjects in several mirror studies. Marchal & Anderson (1993) presented 8 capuchin monkeys with mirrors of varying sizes, including one portable mirror, in the hope that variations of mirror objects and increased control over the reflections would facilitate self-recognition. Riviello, Visalberghi & Blasetti (1992) aimed to capitalise on capuchin monkeys' individual recognition abilities, hoping that group exposure to a mirror might focus the monkeys' attention on the "unfamiliar" monkey in the mirror. Collinge (1989) exposed a large group of capuchins to a mirror for 5 weeks, and found that age and rearing history affected the monkeys' mirror behaviour. Hand-reared individuals directed less social responses at the mirror image, whereas young adults spent more time looking at the mirror then any other age class. However, none of these three studies found indications of MSR in any monkey tested. Nonetheless, capuchin monkeys have been observed to use portable mirrors for 'oblique looks' (Anderson & Roeder, 1989), which has been linked to an increased understanding of mirror properties (Anderson, 1984). A recent study by de Waal, Dindo, Freeman & Hall (2005) compared capuchin monkeys' responses to their own mirror image to responses elicited from familiar or unfamiliar conspecifics. Despite not observing any mirror-mediated self-directed behaviours in response to the mirror image, de Waal and colleagues found that the monkeys treated the mirror image differently to both familiar and unfamiliar conspecifics by directing more direct eye contact and more affiliative behaviours towards the mirror image, suggesting that the mirror image is not perceived as 'just' an unfamiliar conspecific. Even though no evidence indicative of MSR was found in previous studies, capuchins' understanding of mirrors was sought to be increased with the manipulations detailed here, which in turn might prompt behavioural evidence of MSR.

In summary, the purpose of the present experiment was three-fold: first, to investigate if exposure to two mirrors simultaneously might prompt MSR in capuchin monkeys as shown by mirror-mediated self-directed behaviours. Second, to investigate the effects of configurational and reflective properties of mirrors on MSR i.e. whether the mirror's physical properties (for example, shape) or the quality of the reflection (for example, blurred) might further increase the monkeys' interest in and understanding of mirrors as measured by 'oblique looks' and other manipulatory behaviours. Third, to test if monkeys might use both mirrors in combination to gain visual access to body areas that could not be seen with only one mirror, which might indicate competent mirror understanding.

5.4.1. Subjects and housing

Subjects were 2 adult male (Heiji, 9 years; Pigmon, 5 years) and two adult female (Kiki, 7 years; Theta, 7 years) tufted capuchin monkeys (*Cebus apella*), all captive born and free-loaned from the Primate Research Institute, Kyoto University by way of its co-operative research program. Heiji and Pigmon were housed together with another adult female and one juvenile male. Kiki and Theta were housed as a pair. All subjects had previously been exposed to live face-on, live profile and 1-second-delayed face-on views of themselves on video, however all subjects were mirror-naïve. Subjects were not food-deprived, and received their normal food rations after experimental testing.

5.4.2. Procedure

Subjects were individually tested in a test cage (46 x 46 x 52 cm) made of transparent acrylic board. A mirror (30.5 x 22.5 cm) was placed approximately 30 cm in front of the test cage, approximately 10 cm above floor level. Each test session lasted 20 minutes, and each subject received one session per day for six days. In each session a second mirror object was placed inside the cage; the order in which these second mirrors were presented was randomised across subjects. These additional mirror stimuli (10 x 11 cm) were all made out of plastic with one reflective side. One normal (clear) mirror and four altered mirrors were used, the latter either changed in their physical appearance or in the quality of the reflection they gave. The two physically altered mirrors consisted of a mirror with a hole in the middle (ca. 3.5 cm in diameter), and a normal mirror placed inside a closed transparent plastic box (16 x 11 x 4 cm), so that it moved and made a clacking sound when the box was picked up or shaken. Mirrors with altered reflective properties included one covered in semi-translucent foil to give a blurred image, and one covered in red translucent foil to reflect a red image. Four of these mirror objects (normal, hole, blur and red) were covered with clear Plexiglas on both sides to protect them from the monkeys' teeth. In addition, a transparent Plexiglas tile was used as a control stimulus (see Figure 5.1). A video camera positioned above the outside mirror recorded all sessions.

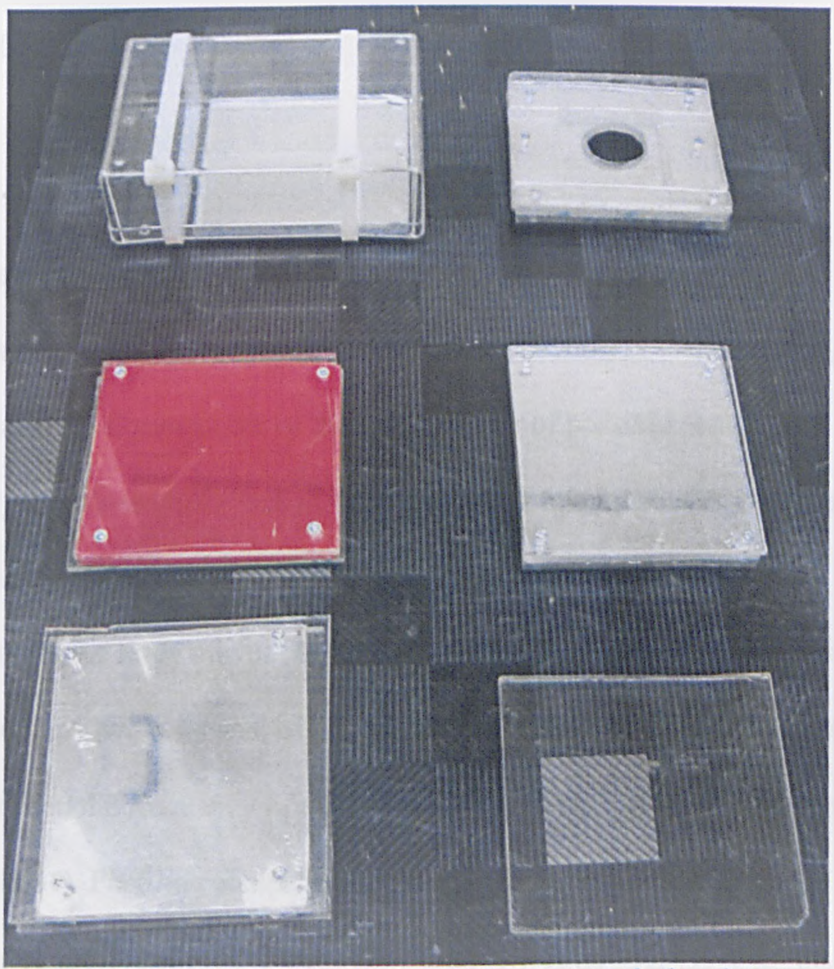

Figure 5.1. The mirror stimuli. Clockwise from top left: box, hole, clear, control, blur, red.

5.4.3. Analysis

Data were coded from the videotapes using one-zero sampling with the observation interval set at 10 seconds. Thirteen predefined types of behaviour were recorded, which fell into 5 broad categories: looking at large mirror, social responses towards large mirror, looking at small mirror, social responses towards small mirror, and manipulation of small mirror (see Table 5.1). In addition, separate notes were taken for any occurrences of mirror-mediated self-directed behaviours, oblique looks, and instances of using both mirrors in combinations. One third (33%) of the sessions was randomly selected and coded a second time to assess reliability. Pearson's correlation of the two data sets showed high agreement between both codings ($r=0.91$, $p<0.001$).

5.5. Results

Figure 5.2 provides a summary of the behavioural categories as shown by the monkeys in each condition. The percentages indicate how often events in each behavioural category occurred out of the total number of possible recorded intervals. Subjects consistently looked most frequently towards the large mirror (44.2% of intervals), followed by looking at the small mirror (17.7%), social responses towards the large mirror (12.7%), and manipulating of the small mirror (6.8%). A Friedman two-way analysis of variance by ranks indicated a significant difference between the frequency of all five behavioural categories (Chi-Square (4) = 72.773, $p<0.001$). Post-hoc comparisons confirmed that looking at the large mirror occurred significantly more frequently than any other behaviour ($z=26.73$, $p<0.05$; Siegel and Castellan, 1988). Social responses towards the small mirror were infrequent, with 7 instances in the normal condition (6 by Kiki, 1 by Heiji) and one instance in the red (Heiji) and box (Kiki) condition. No instances of mirror-mediated self-directed behaviours, oblique looks or use of both mirrors in combination were observed.

Category	Behaviour	Definition
Looking Responses Large Mirror	Look	Looks at large mirror for 1 second or more
	Glance	Looks at large mirror for less than 1 second
Social Responses Large Mirror	Forehead Raise	Raises forehead while looking at large mirror
	Grin	Raises forehead and shows grin while looking at large mirror; may be combined with penile display in males
Looking Responses Small Mirror	Look	Looks at small mirror for 1 second or more (mirror side only)
	Glance	Looks at small mirror for less than 1 second (mirror side only)
Social Responses Small Mirror	Forehead Raise	Raises forehead while looking at small mirror (mirror side only)
	Grin	Raises forehead and shows grin while looking at small mirror (mirror side only); may be combined with penile display in males
Manipulative Responses Small Mirror	Touch	Touches mirror object with hand or foot
	Hold	Picks up mirror object and holds it with both hands
	Mouth / Bite	Inserts mirror object into mouth
	Pull / Push	Pushes or pulls mirror object across the cage floor
	Turn over	Turns over mirror object so that non-reflective side becomes visible (and vice versa)

Table 5.1. Behavioural categories and definitions used to code data

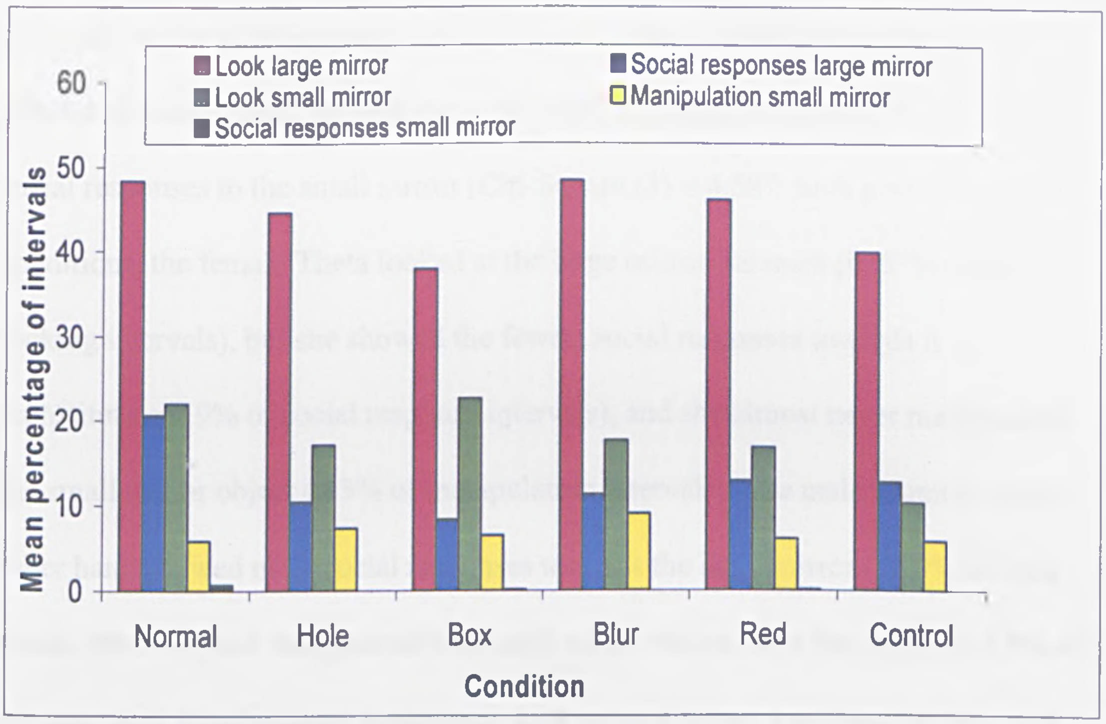

Figure 5.2. Mean percentage of total intervals of each behavioural category summarising all four subjects in each condition.

A Friedman test showed a significant effect of condition on looking responses towards the small mirror (Chi-Square (5) = 13.143, p=0.022). Post-hoc comparisons revealed that as a group, the monkeys looked significantly less at the control object (10.4%) compared to the normal mirror (22.0%), the mirror with hole (17.1%), and the mirror in the box (22.6%; all p < 0.05; Siegel & Castellan, 1988). No significant difference was found between looking at the control object and looking at the blurred mirror, or looking at the red mirror (both p>0.05; see also Figure 5.2). No other effects of condition on the other behavioural categories were found (all p>0.05).

A Kruskal-Wallis test indicated significant differences between individuals for looking at the large mirror (Chi-Square (3) = 8.641, p=0.034), social responses towards the large mirror (Chi-Square (3) = 14.551, p=0.002), and manipulation of the small mirror (Chi-Square (3) = 19.893, $p<0.001$). No differences between individuals were found for looking at the small mirror (Chi-Square (3) = 2.106) or social responses to the small mirror (Chi-Square (3) = 4.587, both $p>0.05$). Across conditions, the female Theta looked at the large mirror the most (in 57% of all looking intervals), but she showed the fewest social responses towards it (constituting 4.9% of social response intervals), and she almost never manipulated the small mirror object (0.3% of manipulation intervals). The male Pigmon on the other hand showed most social responses towards the large mirror (24.9% of total social intervals) and manipulated the small mirror object most frequently (32.8% of all intervals). Manipulatory behaviours took several forms; touching, holding and mouthing the mirror were the most frequent for all monkeys. Looking usually occurred when the small mirrors lay on the floor, but occasionally the monkeys held them against the side of the cage, or raised them high above their heads when looking at them. Heiji occasionally banged the small mirrors against the floor and walls of the test cage whilst holding them in both hands. Among social responses forehead raise (raising of forehead with ears retracted; Weigel, 1978) was far more frequent than grin (forehead raised, ears retracted, mouth corners retracted to show teeth; Weigel, 1978). Only Pigmon showed grin repeatedly towards the large mirror in all conditions.

The average frequency of each behavioural category across sessions was also examined. The number of intervals of looking behaviours towards the large mirror decreased progressively over sessions (from 46.8% in session 1 to 30.0% in session 6; $r_s = -0.439$, $p=0.53$). Although there was a general trend towards a diminishing responsiveness across sessions, the frequency of all other behaviours did not change significantly (see Figure 5.3).

Figure 5.3. Responses of the capuchin monkeys to both mirrors across sessions.

5.6. Discussion and Conclusion: Can capuchin monkeys recognise themselves in a mirror?

As in previous studies with capuchin monkeys (Riviello et al., 1992; Collinge, 1989, Anderson & Marchal, 1993; de Waal et al., 2005) no behaviours indicating self-recognition (such as mirror-mediated self-directed behaviours) were observed. Previous studies also found that mirrors at a right angle resulting in up to three reflections (Anderson, 1983), or simultaneous left and right profile reflections (Anderson & Roeder, 1989), did not elicit MSR in monkeys. The results of the present study extend these findings in that presentation of two mirrors simultaneously (one that could be freely manipulated and one in a fixed location) did not appear to enhance the monkeys' understanding of the reflection, and did not elicit self-directed responses. Moreover, although capuchin monkeys sometimes use mirrors for 'oblique looks' (Anderson & Roeder, 1989), this behaviour did not occur in the present study, nor were there any instances of using both mirrors in combination to look at otherwise visually inaccessible areas. However, more sophisticated forms of mirror use, such as mirror-mediated searching for objects, tend to emerge following extended experience with mirrors (Marchal & Anderson, 1993). Exposure to mirrors was relatively short in the present study (a total of 120 minutes for each monkey). Conceivably these behaviours might have emerged following more extended periods of mirror exposure.

The monkeys showed a range of social and manipulative responses, and as in previous studies (Anderson & Roeder, 1989; Marchal & Anderson, 1993) the large mirror was looked at most frequently, and it elicited the most social responses. Individuals also varied considerably in the frequency of looking, social and manipulative reactions towards the reflections, as has been observed in other studies (Riviello et al., 1993; Collinge, 1989). The younger adult male in particular showed high frequencies of grin, which has been identified as a signal of appeasement or reassurance and serves to avoid aggressive encounters (Weigel, 1978). Forehead raise, which has not been linked to aggressive encounters but is more likely to be used in play contexts, was far more common for the other monkeys (Weigel, 1978). Both grin and forehead raise behaviours indicate that the monkeys perceived their mirror images as conspecifics, and suggest an absence of MSR. It seems likely that factors such as age, sex and dominance status influence how individual monkeys react to their reflections (Hall, 1962; Anderson, 1994), but the present study had too few subjects to draw any firm conclusions about individual factors.

It is interesting that the different properties of the small mirror objects did not affect reactions towards the large mirror. In fact, the greater salience of the large mirror image might have overshadowed differential responses to the small mirror objects. The only behavioural difference between the small mirror conditions was in looking responses. In particular, the objects bearing 'normal' mirror properties (normal, hole, box) but not the 'unusual' mirrors (red, blur) were more frequently looked at than the control object. This result suggests that the differential physical complexity of the mirrors did not enhance the manipulation of these objects, and therefore may be unlikely to increase mirror understanding. Furthermore, there appears to be a visual preference for clearly discernible reflections, which has also been reported in human infants (Schulman & Kaplowitz, 1976).

It has been suggested (e.g. Gallup, 1991) that direct eye contact, which may be perceived as a threat by some primates, might confound the results of self-recognition tasks. The fact that the capuchin monkeys in the present study looked at their normal reflections more frequently may suggest that, at least in these monkeys, direct eye contact was not perceived as a threat but that it enhanced interest (see also Anderson & Roeder, 1989). An aggressive stare may also 'lock' the animal in an aggressive stare-out, therefore increased looking behaviours may also indicate an aggressive basis; however, as all monkeys (apart from Pigmon) showed a majority of affiliative behaviours towards their mirror image, an affiliative basis seems more plausible. It also supports the view that failure to find indications of self-recognition in capuchin monkeys is not due to inadequate experimental designs which preclude possibilities to learn about mirror properties, but is more likely to reflect cognitive limitations in these primates.

In terms of secondary representations the present study did not find any behaviours indicative of secondary representations in capuchin monkeys, which is consistent with the lack of evidence for secondary representational abilities in monkeys found in other studies. This absence of MSR may therefore be caused by a true absence of secondary representational abilities, however as argued above, difficulties in other cognitive areas (which conceivably support MSR) may also preclude the emergence of MSR. Future work on these other factors (particularly monkeys' understanding of mirrors as reflective surfaces) may reveal whether the monkeys' inability to show MSR can solely be attributed to a lack of secondary representational abilities.

5.7. Mirrors as a tool in psychological research with nonhuman primates

Despite the fact the monkeys do not appear to recognise themselves in a mirror (or perhaps specifically due to this fact), mirrors nonetheless are utilizable for psychological studies, and can serve to enhance captive primates' welfare. For example, Anderson (1984) pointed out that mirrors are an ideal tool to investigate social facilitation effects in monkeys without risking serious injury of study animals due to aggression between familiar or unfamiliar conspecifics. Furthermore, mirrors do not pose the same confounds as other (live) animals might, such as the effects of different genders, dominance ranks or social behaviours directed at the study animal. However, mirrors do not appear to have been used frequently in this way and social facilitation effects are still most commonly studied using live animals (e.g. Galloway, Addessi, Fragaszy & Visalberghi, 2005). Mirrors also serve as positive reinforcer for some animals (Anderson, 1984), which may be a useful alternative to standard food and water rewards.

Mirrors can also significantly enhance the welfare of captive primates, particularly primates that have to be singly housed out of other experimental necessities. For example, Anderson (1983) found that a mirror calmed paired-housed infant stumptailed macaques during separation from their peers. Even though many studies found that interest in mirrors may decrease over time (Platt & Thompson, 1985), monkeys nonetheless may spend a small percentage of their time manipulating a mirror after many months of mirror exposure (e.g. Harris & Edwards, 2004). Furthermore, a mirror may represent an otherwise unavailable social partner to single housed monkeys, and can serve to reduce stress and anxiety. For monkeys in close contact with humans, a mirror can be used for 'oblique looks' in order to avoid direct eye contact, which has been discussed as another potential benefit of mirrors (Harris & Edwards, 2004). Thus, far from being unsuitable for monkeys due to their apparent inability to recognise themselves, mirrors are a valuable tool for both primate research and husbandry.

Chapter Summary

In this chapter, mirror self-recognition (MSR) was examined in capuchin monkeys using two simultaneous mirror objects. Furthermore, the effects of different mirror properties (alterations in either the shape or reflection of the mirror) on mirror understanding were studied. These manipulations were thought to potentially increase the monkeys' understanding of mirrors as reflective objects, thereby prompting MSR. Results showed that the monkeys engaged in more eye contact with their clear mirror images than with control stimuli, however no behaviours indicative of MSR were observed. These results suggest that alterations of the mirror object are unlikely to increase mirror understanding, and that failure of MSR in monkeys could potentially be due to a true lack of secondary representational abilities. Mirror objects are nonetheless considered a useful tool for comparative research and animal welfare.

Chapter 6 – Means-Ends Reasoning in Capuchin Monkeys

In this final experimental chapter, capuchin monkeys' ability to use secondary representations in the context of means-ends problem solving will be examined. Means-ends reasoning has previously been studied in detail with regards to tool use, however the presented work will look at means-ends reasoning outside of tool-using contexts. In this chapter, the role of secondary representations in means-ends reasoning will be explained, followed by a brief review of evidence for means-ends reasoning in human and nonhuman primates. Two experiments are then presented aimed at examining means-ends abilities in a visual search task, concluding with an evaluation of the capuchins' performance in terms of secondary representational abilities.

6.1. Means-ends reasoning and secondary representations

Secondary representations, which are removed from the immediate reality and therefore can model past, future or entirely hypothetical situations, appear to be a crucial component in advanced means-end reasoning and goal-directed behaviours. For example, Perner (1991) argued that when considering how to solve a novel problem a solution might be derived by relating the primary represented problem state to a desired secondary represented goal state, and to use other secondary representations to conceive of intermediate steps to achieve the desired goal state (e.g. Piaget, 1954; Fabricius, 1988; Suddendorf & Whiten, 2001). Of course, not all problem-solving relies on planning abilities, and problem-solving may be achieved through trial-and-error learning. However, trial-and-error learning may be slow and costly to an individual, whereas planning might reduce these costs (Bauer, Schwade, Wewerka & Delaney, 1999). The use of secondary representations in problem solving can be inferred by the sudden appearance of a solution (also called insight; Koehler, 1957), rather than the slow, gradual trial-and-error acquisition of a skill. Hence, the form in which a problem is solved by an individual can serve as an indicator of secondary representational abilities.

Forward planning in relation to problem solving does not necessarily imply a projection of oneself onto the future goal state, and therefore does not fall under the future planning abilities as stated by the Bischof-Koehler hypothesis. The Bischof-Koehler hypothesis claims that no animals other than humans can anticipate future needs, drives or other motivational states (Suddendorf & Corballis, 1997). Anticipating future needs is a metarepresentational capacity, because one's own mental states need to be conceived of in a hypothetical situation, thereby explicitly representing a representational medium (mind) and how it relates to the environmental situation. However, future planning as used in the current context may not require any anticipation of future needs and drives. In fact, planning in the present context refers to solving a currently presented problem with the end to satisfy a currently experienced need. It can therefore be achieved through the use of secondary representations depicting the goal state, which are used alongside primary representations of the problem state.

6.2. Means-ends reasoning in human infants

Means-ends problem solving has been studied in human infants using object permanence tasks, or tasks involving steps or sequences of actions to achieve a specified goal. For example in classic invisible displacement tasks infants are shown a desirable toy, which is then placed into a box or container. The container is then moved under a cloth or a second container, and when the first container is removed again from the second container it is shown to the infant to be empty. The infant's task is to find the toy. For an individual only capable of primary representations, this task is a puzzle. Primary representations cannot represent where the toy has been, and therefore infants cannot conceive of its possible location under the second container. However, secondary representations allow the infant to re-construct the toy's path from inside the first container to under the second container followed by its 'disappearance' at the final inspection. Hence infants can conceive of the toy's last location within the second container, and successfully search at the toy's last known location. Infants generally pass invisible displacement tasks at the age of 15-18 months (Haake & Somerville, 1985).

Other studies have shown that by 2 years of age infants can follow a sequence of actions in order to achieve a final goal state. Bauer et al. (1999) presented four different problem states to infants, which could be solved by following sequential steps towards the desired goal state. For example, infants were shown the final step in producing a rattle out of two small plastic barrels and a small wooden block (a three step sequence was required to achieve this end state), and subsequently given the opportunity to produce a rattle themselves. Even children aged 20-21 months were more likely to produce this end state based on seeing the final step alone compared to children who were only shown the finished product, which has been interpreted as active planning of sequential steps towards a goal state (Bauer et al., 1999), most likely based on secondary representational abilities.

Indirect evidence also supports the view that infants aged 1.5-2 years develop planning abilities. For example, Bullock & Lutkenhaus (1988) analysed 15-35 month old infants' monitoring, controlling and correcting behaviours and affective reactions in relation to play and clean-up tasks, and found that at 20-26 months of age infants showed clear evidence of paying attention to the production of outcomes per se, accompanied by signs of pleasure. Similarly, Kagan (1981) observed that at 20 months, infants frequently smiled when completing a goal-directed action, or displayed negative reactions when failing to complete a goal-directed action. Both these findings show that children react differently to achieved and not achieved goals, suggesting that the goal state is projected during the problem situation and is subsequently evaluated in comparison to the actual outcome of the infants' actions. These converging findings suggest that means-ends reasoning develops at around 1.5-2 years in infants, at the same time that other abilities emerge that are considered to be reliant on secondary representations (such as mirror self-recognition; Amsterdam, 1972).

6.3. Means-ends reasoning in apes

Classic experiments on problem-solving abilities in primates often involve the employment of tools to obtain a food reward. For example, in Koehler's (1957) experiments, chimpanzees had to stack a series of boxes to reach a banana hanging from the ceiling or combine two sticks to rake in bananas into reach from outside the cage. These sequential behaviours to achieve a goal have been interpreted as evidence that the chimpanzees represent the final goal (obtain banana), and are capable of entertaining intermediate sub goals (e.g. climb boxes) in relation to the final outcome. Crucially, solutions to these problems sometimes emerge suddenly and not after an extended period of random manipulations, which has led to the term 'insight' being used for rapidly acquired problem solutions in the absence of trial-and-error learning (Koehler, 1957). A different approach to investigate planning abilities in primates was taken by Dunbar (2000), who presented chimpanzees and orang-utans with a puzzle box outside of their cages. When subsequently given access to these puzzle boxes, chimpanzees and orang-utans who had previously been exposed to the boxes were faster to open them than individuals that did not have any prior opportunity to look at the boxes. Dunbar (2000) interpreted these findings as showing that the apes mentally worked through the puzzle boxes (supposedly using secondary representations), however subsequent studies failed to replicate the results (only children and not apes had faster solution times when exposed to the boxes; Dunbar, McAdam & O'Connell, 2005).

Experiments on object permanence also show that both orang-utans and chimpanzees can pass invisible displacement tasks. Call (2001) presented adult apes and 19-26 month old children with three containers. A food reward was placed under a small box, which was then passed under three containers. All three species successfully retrieved the reward after it had been displaced invisibly, however all species exhibited difficulties with double non-adjacent invisible displacements (i.e., when the reward was passed from the small box to container 1, and subsequently to container 3). Call (2001) interpreted these results as showing general object permanence skills in great apes, but difficulties with response bias and inhibitory control, which implies that apes, using secondary representations, can conceive of the reward's past or possible locations (see Natale et al., 1986, for similar results with a female gorilla).

There is also evidence that chimpanzees can plan to achieve a future goal outside of laboratory settings. Field observations have shown that chimpanzees transport stones to nut-cracking sites (e.g. Boesch & Boesch, 1983; 1984), which may be based on secondary representations of the nut-cracking site whilst in a separate nut-cracking tool location. Furthermore, chimpanzees have been observed to use tool sequences (Boesch & Boesch, 1990; Brewer & McGrew, 1990; Sugiyama, 1995) and even 'metatools' (Matsuzawa, 1991), thus supposedly representing the future appearance of an object whilst manipulating it. Although one cannot exclude the possibility that these behaviours came about by no more than associative learning (after all, the chimpanzees might have had extended trial-and-error learning opportunities while not being observed), they are line with findings from laboratory studies suggestive of general means-ends reasoning abilities in great apes.

6.4. Means-ends reasoning in monkeys

Means-ends reasoning in monkeys in the form of insightful tool use has been most intensely studied by Visalberghi and colleagues. Capuchin monkeys were presented with a clear plastic tube, which contained a reward that could only be reached by inserting sticks to push the reward out of the tube. While capuchin monkeys readily used a stick to obtain the reward, which might have been interpreted as showing that the monkeys were conceiving the solution of the problem, their understanding of their own tool use behaviour was further probed by the presentation of tools that needed to be manipulated before they could be used. Visalberghi & Trinca (1989) provided the capuchins with a bundle of sticks (to be broken apart before insertion), three short sticks (to be inserted sequentially into the same side of the tube), and a stick with two transverse pieces (to be removed before insertion). Even though the capuchins readily handled all tools and eventually managed to obtain the reward, the patterns of their errors suggests that they did not conceive of an end state and did not systematically follow a route of intermediate steps to obtain the desired outcome. For example, the capuchins repeatedly attempted to insert the entire bundle into the tube, inserted two short sticks into opposite ends of the tube, or inserted a small piece of tape into the tube, all clearly not altering the location of the reward, before checking the opening of the tube as if expecting the reward to be available.

Visalberghi & Limongelli (1994) further assessed the capuchins' insight into their own actions by presenting them with a 'trap' in the middle of the tube. If the reward was pushed into the trap, it fell into a small container and became unavailable. Through a series of trials, only one monkey out of four avoided the trap above chance levels, suggesting that most of them did not monitor the likely consequences of their manipulations. Furthermore, when the trap was made ineffective by rotating it, the previously successful monkey continued to avoid it, perhaps not anticipating that the reward would still be available if it passed underneath the trap. Visalberghi & Limongelli (1994) interpreted these findings as suggestive of an application of a distance-based rule between stick, reward and trap rather than an causal understanding of the problem in the sense of "moving (mentally) forward and backward in time" (Fragaszy et al., 2004, pp. 198). In other words, the results of the tube experiments suggest that capuchins, despite being highly proficient and frequent tool users (at least in captivity), learn successful tool use behaviours through trial-and-error learning in which the correct response is gradually reinforced

(Visalberghi & Limongelli, 1994, 1996; Visalberghi, 1997, 2000; Visalberghi & Tomasello, 1998; Fragaszy et al., 2004).

Even though the tube studies appear to suggest a failure of means-ends reasoning in capuchins and accordingly a lack of secondary representations, similar studies with chimpanzees suggest that success on tube tasks may not be a straightforward secondary representational achievement. For example, Visalberghi et al. (1995) gave parts of the original (Visalberghi & Trinca, 1989) tube problems to five chimpanzees. Even though the chimpanzees were judged to have 'more foresight' when solving this task because they did not attempt to insert the whole bundle and solved the problem at the first trial, they nonetheless made a large number of errors (such as inserting small, ineffective sticks) which even increased across trials for two of the chimpanzees. Furthermore, when Bard, Fragaszy & Visalberghi (1995) administered the task to younger chimpanzees including the short stick condition, the chimpanzees made more errors during later trials, suggesting that they also failed to understand the causal relations involved. These results are surprising given that chimpanzees pass other tasks suggestive of means-ends reasoning and secondary representations (see above), and may in turn suggest that the tube task may require other abilities besides secondary representations.

Object permanence and invisible displacement tasks, which may provide a more rigorous test of secondary representational means-ends reasoning, may therefore be more useful for assessing monkey's abilities of means-ends reasoning. Invisible displacements have been investigated in several monkey species, including Japanese macaques (Natale et al., 1986), longtail macaques and capuchin monkeys (Natale &

Antinucci, 1989). For example, Natale & Antinucci (1989) presented their subjects with one small and two larger objects. A reward was placed underneath the smaller container, which was then placed underneath one of the larger containers. When the smaller container re-emerged, it was shown to be empty. Both macaques and capuchins showed a tendency to search under the correct container, however when some additional gestures were introduced so that all containers were touched by the experimenter the monkeys often searched under the third container, even though it was impossible that the reward could have been deposited there. Using these tighter controls, capuchins were judged to have failed the invisible displacement task (Natale & Antinucci, 1989; Tomasello & Call, 1997).

What about examples from wild populations? Fragaszy, Izar, Visalberghi, Ottoni & de Oliveira (2004) surveyed a capuchin monkey nut cracking site in Brazil, and found that the monkeys used river stones which were not found in the local area to crack open nuts. Fragaszy et al. (2004) suggested that these stones were probably transported to the nut cracking site by the capuchins. Studies in the laboratory confirmed that capuchins may transport tools to a nut cracking site, or nuts to a tool site if there are no suitable tools at the site already (Jalles-Filho, Grassetto, de Cunha & Salm, 2001; Cleveland, Rocca, Wendt & Westergaard, 2004). These findings challenge the previous negative findings about monkeys' means-end reasoning, and suggest at least some projection of future goals in monkeys.

6.5. Means-ends reasoning outside of object manipulation contexts

As outlined above, human infants and to a certain extent apes appear capable of projecting a goal of an action by means of secondary representations and following intermediate steps to achieve the final goal in both invisible displacement and tool use experiments. The results for monkeys are mostly negative – they fail invisible displacement tasks and appear to employ learned associations in tool-using contexts, but transport tools to nut cracking sites in both the lab and in the wild. However, all three contexts require manipulations of objects – retrieving rewards from under boxes, pushing a reward out of a tube, or transporting tools between sites. These similarities might be regarded as a common confound in all three contexts; perhaps monkeys have difficulties in understanding objects and their causal relations with each other, rather than failing to project the outcome of their manipulation behaviours.

In order to avoid this confound one might test monkeys in contexts in which they could project a goal or work through a series of steps to achieve a goal, and which do not involve the use of tools. At the same time other factors which might compromise the monkeys' abilities should also be avoided – for example, contexts that rely on theory of mind abilities (a metarepresentational achievement; see Chapter 1). Recent studies investigating visual search strategies appear to be suitable for this purpose.

Visual search strategies can be regarded as relying on goal projection and thereby secondary representational abilities. For example, when searching for an item of food, searching ceases once the item has been found, thus potentially showing that the specified goal has been achieved. However, searching for food in itself may be instinctively governed without the need for secondary represented goals, i.e. an individual may engage in food searches on the basis of instinctive drives without explicitly representing what item it is searching for. Hence, searching in itself is not sufficient to demonstrate explicitly represented goals. A better way of investigation is to analyse an individual's search patterns, where and under what circumstances are searches initiated or concluded, in order to draw conclusions about goal representations. If an individual can make inferences about locations that have yet to be searched based on what they have previously seen in other potential hiding places, then these inferences would be strong indicators that the individual represented the goal state in itself. For example, if an individual chooses a visually uninspected hiding place after having visually inspected all the other empty hiding places, one can reason that the subject has inferred the location of a hidden object or food reward based on the representation of that object. Furthermore, the search strategies employed (whether searches are efficient or redundant) can indicate the degree to which a subject can plan and keep track of already searched and depleted hiding places. Importantly for all these premises, searching and finding/obtaining an object need to be clearly dissociated during the object search task, i.e. an individual should not be able to search and obtain an object at the same time. If searching and finding are confounded, it is not possible to differentiate between searches initiated through instinctive drives and searches initiated on the basis of explicitly represented goal states.

Studies addressing these issues have been conducted fairly recently with human infants, apes and monkeys. Call & Carpenter (2001) showed hollow tubes, one containing a food reward, to 2.5-year-old human infants, chimpanzees and orang-utans who were allowed to look into the tubes before selecting one (thereby dissociating searching from obtaining). They received the reward only if they selected the baited tube. Call & Carpenter (2001) found that all three species were efficient with their searches: they tended to search only when necessary, i.e. when they had not previously been informed about the bait location through a visible baiting gesture by the experimenter. Searching in the absence of knowing the bait location also increased the chances of success. Importantly, all three species engaged in 'super-efficient' searches, i.e. selecting the third tube without prior visual inspection if the other tubes were found to be empty, although they did so only infrequently and preferred to locate the bait by searching instead. Nonetheless, these 'super-efficient' searches suggest that all three species were explicitly representing a goal state, and were going through intermediate steps to achieve this goal. Hampton, Zivin & Murray (2004) adapted the tube paradigm to test rhesus macaques. Like humans and apes, the macaques searched more when they had not witnessed the baiting, and selection accuracy increased when they searched. However, no mention of 'super-efficient' search strategies was made (Hampton et al., 2004), suggesting a failure to explicitly represent a goal state.

In the present series of experiments, the tube paradigm was adapted for investigating capuchin monkeys' spontaneous search strategies. Capuchins have previously been tested in a similar task by Grether & Maslow (1937), who investigated this species' abilities of deduction. Two cups were placed in front of the monkeys, and one cup was shown to be empty. The monkeys' task was simply to choose the baited cup, which they easily did. All four capuchins arrived at this solution quickly, although the presented data do not indicate if the monkeys completed tests correctly on the first trial. Furthermore, one monkey transferred the correct choice behaviour to 3- and 4-cup problems. These results are promising in that capuchins appear capable of deducing the correct bait location, however the selection of the correct cup could also have been brought about by simple associations involving the experimenter's contact with the incorrect cup. Furthermore no search behaviours were executed by the monkeys, which may have given more insight into the monkeys' strategies to achieve a goal. Other studies have shown that capuchins will efficiently deplete an array of food containers whilst minimising travel distance between them (de Lillo, Visalberghi & Aversano, 1997; de Lillo, Aversano, Tuci, & Visalberghi, 1998), suggesting a degree of forward planning in capuchins' search behaviours. However, as searching and obtaining the reward was confounded in these latter experiments, it is difficult to evaluate the influence of an explicitly represented goal on the monkeys' foraging behaviour. Together the available data suggest that capuchins may be capable of explicitly representing a goal whilst planning a series of intervening steps. The following experiments were conducted to test this hypothesis more directly.

6.6. Visual search strategies in capuchin monkeys

The present experiment follows those by Call & Carpenter (2001) and Hampton et al. (2004). Capuchin monkeys were presented with a visual search task in which search behaviour and obtaining the reward were functionally separated. The monkeys were presented with three tubes, one of which was baited, and the monkeys' task was to select the baited tube in order to receive the bait. The capuchins' search strategies were analysed with regard to their search efficiency and the effect of additional information about bait location. Particular attention was paid to any instances of 'super-efficient' searches (selecting a tube without searching it after finding the other tubes empty).

6.6.1. Subjects and housing

Subjects were one adult male (Heiji, 9 years), three adult female (Kiki, 7 years; Theta, 7 years; Zilla, 9 years) and one juvenile male (Zinnia, 2 years) tufted capuchin monkeys (*Cebus apella*), all captive-born and on loan from the Primate Research Institute, Kyoto University by way of its cooperative research program. Heiji, Zilla and Zinnia were housed together with a young adult male; Kiki and Theta were housed as a pair. Three monkeys (Heiji, Zilla and Theta) had previously participated in object discrimination tasks, and had been trained to use a pointing/reaching gesture to indicate their selections. Zilla was pregnant throughout the experimental period and gave birth four weeks after completion of the experiment. The monkeys were not food deprived, but received part of their daily food rations during testing.

6.6.2. Apparatus

All monkeys were tested individually in a familiar testing cage made out of transparent acrylic board (46 x 46 x 52 cm). At the front of the cage was an opening (23.5 x 3.5 cm), ca. 5cm above the floor. This allowed the monkeys to reach out toward three plastic tubes (40 x 5 cm diameter) that were fastened on a platform and held in position by wooden rails spaced 8 cm apart and perpendicular to the test cage. During testing, the tubes were raised ca. 3 cm at the end furthest from the monkey, so that it was only possible for the monkey to look through one tube at a time. The platform was situated on a small table (59.5 x 45.5 x 30 cm) that was level with the floor of the cage. A white cardboard screen was placed between the apparatus and the test cage when required to occlude the baiting process (see also Figure 6.1).

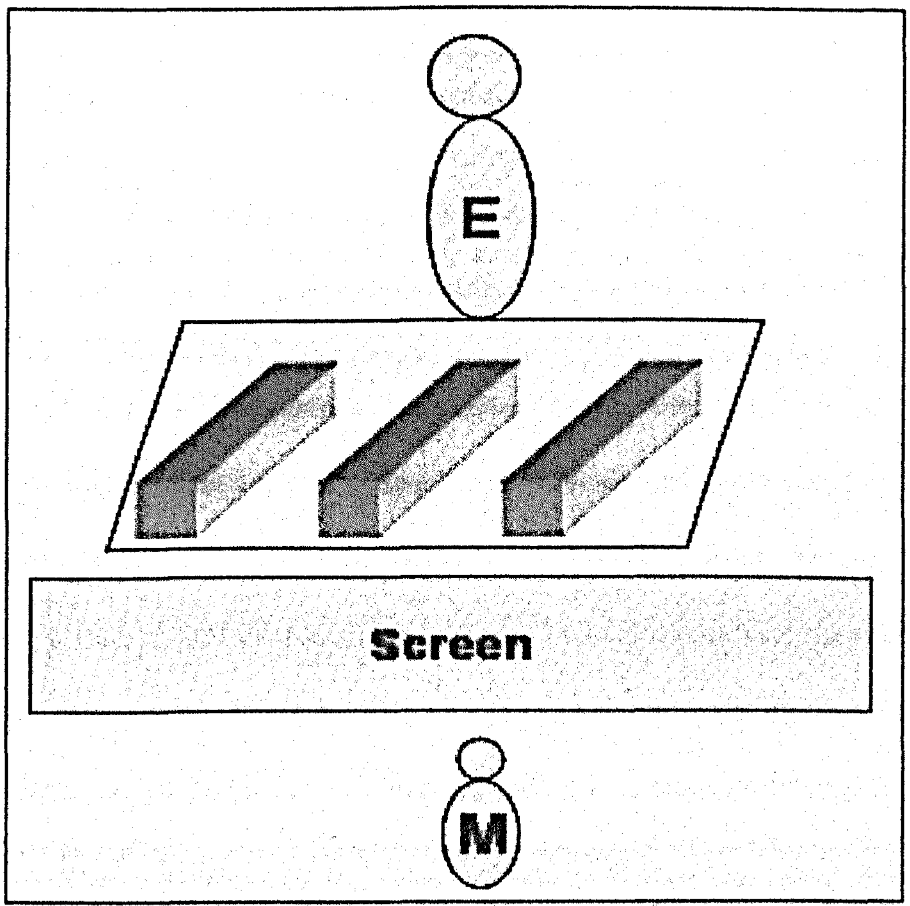

Figure 6.1. Schematic diagram of set-up

6.6.3. Preliminary training

Monkeys were given between 3 and 8 preliminary training sessions to familiarise them with the testing procedure and to establish a reaching response toward the tubes. During training the openings of the tubes facing the monkey were blocked with a small piece of white cardboard, so that the monkey would not learn to look into the tubes. The experimenter sat behind the apparatus facing the monkey with the screen occluding both the experimenter and the apparatus. In order to minimise any unintentional cueing of the correct response the experimenter remained passive and visually focused on the opening of the test cage throughout the experiment.

Each trial started with the screen being removed and a small piece of apple or sweet potato (the bait) being visibly put on top of one of the three opaque tubes. If the monkey reached toward the baited tube, it received the bait and the trial was ended by replacing the screen. If the monkey reached toward a non-baited tube, no reward was given and the screen was replaced immediately. Reaching was simply defined as an extension of the arm toward a tube as if the monkey was trying to touch the tube. Occasionally, the monkeys would tap the table in front of a tube, which was also considered an acceptable selection response. In the second training phase, several false baiting gestures were added so that all tubes were touched once in random order but only one tube was baited. For the final training phase, the experimenter placed the bait on top of one tube before removing the screen with the platform situated 35 cm in front of the test cage. After removing the screen, the platform was pushed ca. 5 cm toward but still out of reach of the monkey. The first reach after the platform came to a halt was taken as the response. Training sessions were administered once a day and lasted ca. 20 minutes per monkey.

Once the monkeys were responding reliably, a more formal evaluation was conducted to make sure that they understood the task. Each test session consisted of 24 trials. In 16 trials the baiting was visible i.e. the screen was removed before baiting so that the monkeys could see the baiting gesture. The remaining 8 trials were unseen, i.e. the bait was placed on top of one tube before the screen was removed so that the monkeys did not see the baiting gesture. Each monkey was judged to have reached criterion when it responded correctly on a total of at least 20 trials per session (over 80% correct). Kiki and Zilla required 3 preliminary training sessions reach criterion. Heiji and Theta required 4 sessions, and Zinnia 8.

Before the actual experiment the cardboard blocking visual access to the inside of the tubes was removed, and the tubes were presented to the monkeys. All the monkeys showed interest in the tubes, and looked through them several times.

6.6.4. Pilot study

In a pilot study a procedure identical to that used by Call & Carpenter (2001) and Hampton et al. (2004) was adopted. The bait was placed inside a tube so that it was not directly visible. The monkeys were then presented with two different types of trials: seen trials, in which the monkeys saw which tube the experimenter baited; and unseen trials, in which the monkeys did not observe the baiting. It was hypothesised that if they were explicitly representing the goal of the task the monkeys might avoid searching tubes when the baiting was witnessed. Furthermore, when the baiting was not witnessed and subjects encountered two empty tubes, they might select the third tube without searching it first. However, problems were encountered with the visible/invisible baiting procedure. In seen trials the monkeys immediately visually followed the food reward during baiting and looked into the baited tube, but even when the experimenter had deposited the reward and, with a clearly empty hand, touched the top of other (empty) tubes, the monkeys continued to look into whichever tube was being touched. It is not clear if the baiting was perhaps too salient for the capuchins to ignore so that they appeared to be unable to visually disengage from the experimenter's hand. Searching a tube was therefore influenced by the experimenter's baiting gesture, and became a confound to the experimental paradigm.

To provide the monkeys with explicit information about the bait location without using a baiting gesture, the procedure was adjusted so that a tube was always baited while the screen was between monkey and apparatus, and two different types of tubes were employed. One type (as used during training and the preliminary experiment) was green-opaque and required the monkey to crouch down to visually check its contents. The second type of tube was transparent, which meant that the monkey could see directly if it was baited. Thus, if explicitly representing the goal of the task, monkeys might search opaque tubes (but not transparent ones because they could directly obtain all necessary information without searching it), and select an opaque tubes without searching if all other tubes were found to be empty.

6.6.5. Procedure

At the start of each trial the experimenter sat behind the apparatus, facing the monkey with the screen in place occluding experimenter and apparatus. The experimenter touched all three tubes in random order to eliminate any sound or movement cues, and the bait was placed inside one of the tubes, at the end furthest from the monkey. The screen was then removed and the platform was pushed toward the monkey after a 5-sec delay. The first reach after the platform came to a halt was taken as the response. If the monkey reached toward the baited tube, the experimenter retrieved the bait, gave it to the monkey and replaced the screen. If the monkey reached toward an unbaited tube, the screen was replaced immediately. If no response occurred after 60 sec the screen was replaced, the bait was retrieved from the tube and the next trial started. Trials were separated by a 5-sec inter-trial interval. A video camera placed behind the experimenter recorded all sessions.

Each monkey received a total of 72 trials in three sessions of 24 trials each, which were conducted once a day on three consecutive days. This relatively small number of trials was intended to prevent an improvement in performance based on learned associations between search behaviours and food rewards. Each monkey received 54 trials in which two opaque tubes and one transparent tube were used, with the location of the transparent tube and the bait counterbalanced across trials. When the transparent tube was baited the monkeys could directly see the bait, so that (if explicitly representing this goal of finding the bait) no searching was required before choosing correctly. On the other hand, when one of the opaque tubes was baited, the monkey could immediately see that the transparent tube was empty and (if explicitly representing this goal of finding the bait) could restrict its searches to the opaque tubes. On the remaining 18 trials one opaque and two transparent tubes were used, with bait and tube locations again counterbalanced. If a transparent tube was baited in these trials, the monkey again could see the bait immediately, so no searches were necessary. If the opaque tube was baited, the monkey could see that the other two tubes were empty. Therefore, the monkey might deduce the location of the bait, and choose correctly without any need for searching. The order of trial types was randomised with the only restriction being that the bait was not hidden at the same location on more than 2 consecutive trials.

6.6.6. Analysis

All sessions were videotaped for later analysis. Baiting gestures were not included in the footage, which allowed blind scoring of the monkeys' behaviours. The number of looks, the tubes that were looked into and the order in which the tubes were looked into were recorded from the moment the screen was removed until selection occurred. Forty percent of trials were coded a second time to assess intra-observer reliability; consistency between codings was high (Pearson's correlations:

r = 0.92, p<0.001 for searches; r = 0.96, p<0.001 for selection). Due to the small number of subjects, results were analysed separately for each individual using non-parametric tests.

6.7. Results

6.7.1. Selection behaviour

All monkeys selected a tube on all trials, but only three monkeys (Zilla, Heiji, Kiki) chose the correct tube significantly above chance throughout the experiment (chance=33%, binomial tests: all p<0.001). The remaining two monkeys showed strong location biases: Zinnia preferentially selected the middle tube (61 selections out of 72) whilst Theta avoided the middle tube (7 selections out of 72). However, although Theta's overall choices appeared random (29 correct out of 72), she chose the correct transparent tubes significantly above chance (15 correct out of 27, binomial test: p=0.011). Since only three monkeys completed the overall task successfully, only these monkeys' data are considered in detail.

The visibility of the bait did not influence the outcome of a trial. All three monkeys were equally successful when the bait was placed inside a transparent tube (100%, 88.9%, and 100% correct respectively for Zilla, Heiji and Kiki) and when it was placed inside an opaque tube (95.6%, 95.6%, and 97.8% correct respectively).

6.7.2. Search behaviour

Zilla, Heiji and Kiki searched on the first trial, and continued to search in at least one tube during all subsequent trials. Typically the monkeys searched until they saw the bait and then either made a selection (47.2%, 50% and 65.3% of trials), or they continued to search but returned to search in the baited tube with their last look before making a selection (12.5%, 18.1% and 16.7% of trials respectively).

Figure 6.2 shows the average number of looks per tube per trial according to bait location and tube searched. The monkeys did not make fewer searches when the bait was directly visible compared to trials when it was not directly visible (Mann-Whitney tests for each individual: Heiji: $z=1.578$; Kiki: $z=-0.56$; Zilla: $z=-1.127$, all $p>0.05$). When comparing the number of looks into the transparent tubes and the opaque tubes during each trial (taking into account the unequal number of tubes), no monkey looked less into the former (68, 61 and 66 looks in total) than into the latter (80, 70 and 69 looks in total, respectively; Wilcoxon Signed Rank tests: Heiji: $z=-1.547$, Kiki: $z=-1.652$, Zilla: $z=0.520$, all $p>0.05$). Selection accuracy was not associated with increased number of looks (correct selections: mean number of looks=3.0, 2.7 and 2.8 for Heiji, Kiki and Zilla respectively; incorrect selections: mean number of looks = 3.0, 2.0 and 3.6 respectively; Mann-Whitney tests: $z=-0.077$, $z=-0.808$ and $z=-1.842$ respectively, all $p>0.05$). In trials with two empty transparent tubes and a baited opaque tube, monkeys never selected the opaque tube without searching in at least one tube first.

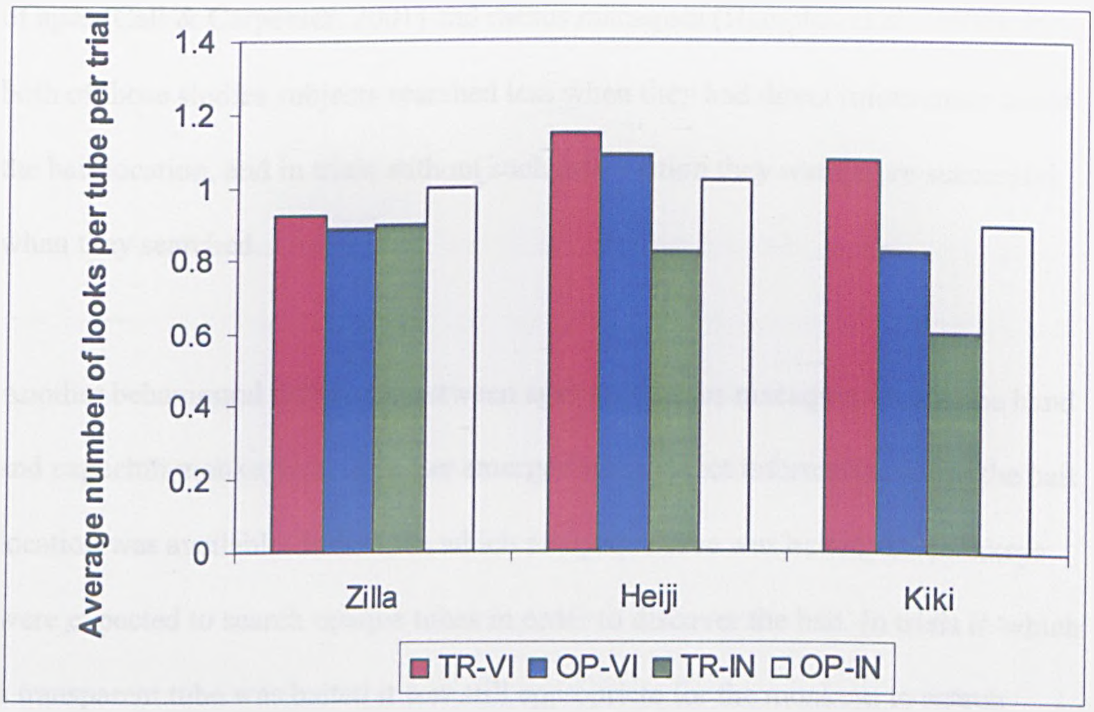

Figure 6.2. Experiment 1 – average number of looks per tube per trial according to baiting conditions. TR-VI: looks into transparent tubes with bait in transparent tube; OP-VI: looks into opaque tubes with bait in transparent tube; TR-IN: looks into transparent tube with bait in opaque tube; OP-IN: looks into opaque tubes with bait in opaque tube.

6.8. Discussion

Although all five monkeys were successful during training, only three monkeys selected the correct tube significantly above chance during the experiment. Seeing the bait directly did not reduce the number of searches, and when the bait location was unknown more searching did not lead to greater success. The lack of association between searching and correct selections by the three capuchin monkeys can perhaps be attributed to selection of the correct tube at ceiling levels, i.e. there were too few incorrect trials to analyse. The two monkeys that failed to reliably select the correct tube also did not search reliably, again making it impossible to match searching behaviour to successful outcomes. These results contrast with those of apes (Call & Carpenter, 2001) and rhesus macaques (Hampton et al., 2004). In both of those studies subjects searched less when they had direct information about the bait location, and in trials without such information they were more successful when they searched.

Another behavioural difference between apes and rhesus macaques on the one hand and capuchin monkeys on the other emerged when direct information about the bait location was available. In trials in which an opaque tube was baited, the monkeys were expected to search opaque tubes in order to discover the bait. In trials in which a transparent tube was baited it was still appropriate for the monkeys to search opaque tubes, perhaps to check if a second bait was available in one of the tubes. Both of these search strategies are consistent with explicitly representing a goal state, i.e. searching until the relevant information has been obtained. However, it is not clear why the monkeys searched transparent tubes when they could directly see the contents of these tubes, and therefore should be aware of the relevant information. In contrast, both apes and rhesus macaques searched less in seen trials when direct information about the bait location was available. A simple explanation for the capuchin monkeys' unnecessary searches could be that they failed to notice the bait inside the transparent tubes. However, one monkey (Theta) reliably selected the correct tube only if it was transparent, which makes this explanation unlikely. Searching in transparent tubes suggests that the capuchin monkeys failed to effectively act on the outcome of their own visual search behaviour, which implies a failure to represent a desired goal state.

One important aspect of the experimental set-up used for testing capuchin monkeys, however, may have significantly impacted on the results of the present experiment. Whereas rhesus macaques and apes both encountered visible baiting gestures, the capuchins received the additional information of the bait's location through the use of transparent tubes. In order to successfully complete the task, capuchin monkeys therefore needed to understand the concept of transparency, a requirement not posed by the visible baiting gesture. Even human infants encounter difficulties with understanding transparency and object relations that involve placement of objects into other objects. For example, infants who pass visible displacement tasks may nonetheless fail invisible displacement tasks that are conducted using transparent cups that clearly show the object to the infant (Bower, 1974). One possible explanation, therefore, is that the capuchin monkeys failed to appreciate that the bait inside the tube was the same bait that was visible when looking through the tube. Even to the one monkey who in the absence of search behaviours chose a correct transparent tube, the bait may have been no more than a discriminative marker without an understanding that it was actually the same bait. Therefore the excessive search behaviour of the capuchins may be caused by a failure to understand the nature of the transparent tubes. However, the fact that these capuchin monkeys were highly familiar with transparent surfaces (e.g. the test cage was made out of transparent plastic), makes it unlikely that the monkeys' inefficient search behaviour was caused by a failure to understand transparent surfaces.

Excessive search behaviour on every trial led to an absence of what Call & Carpenter (2001) termed 'super-efficient' searches, that is, selecting a tube by inference based on indirect knowledge gained about the bait location rather than seeing the bait (either directly or through searching), which may suggest a failure to project the goal of the search behaviour. However, 'super-efficient' searches were not strictly required to solve the task successfully, so an absence does not necessarily imply an inability to perform these searches. Call & Carpenter (2001) found 'super-efficient' searches in both 2.5-year-old human infants and apes, however both species engaged in 'super-efficient' searches only infrequently and preferred to locate the bait by searching instead. To test more directly if capuchin monkeys can predict the location of a reward, Experiment 2 was designed in which successful task performance depended upon tube selection without seeing the bait.

6.9. Deduction of a bait location in capuchin monkeys

In Experiment 2, one opaque tube with the end bent 90 degrees was introduced. When this tube was baited, the bait could not been seen by looking into the tube. Hence unlike the straight opaque tubes in Experiment 1, this bent tube offered no information about the bait location. In addition, the monkeys could easily identify this tube before searching. This set-up therefore provided the opportunity to investigate if capuchin monkeys could predict the location of a bait based on indirect information (i.e. excluding all other possibilities). The first question was whether the capuchin monkeys would infer the bait location within the bent tube and select it if they could not see the bait in either of the other tubes. The second question was whether they could do so without searching the bent tube first, which would show that the monkeys recognised the futility of searching the bent tube.

6.9.1. Subjects, apparatus and procedure

The same five monkeys from the previous experiment were tested, and the same basic procedure was used. The apparatus consisted of one 90-degree horizontally bent opaque tube (42 x 5 cm) and two straight opaque tubes. The locations of the bent tube and the bait were randomised across trials, with the only restriction that the bait was not in the same location on more than two consecutive trials. Monkeys received one test session of 32 trials. On 12 of those trials the bait was hidden in the bent tube. Prior to the start of the experiment, the experimenter held up the bent tube in front of the monkeys; all monkeys inspected the tube and looked into it several times. Data were collected and analysed as in Experiment 1. Forty percent of trials were coded a second time; intra-observer reliability between codings was high (Pearson's correlation: $r = 0.94$, $p<0.001$ for searches; $r = 0.98$, $p<0.001$ for selection).

6.10. Results

6.10.1. Selection behaviour

Kiki, Zinnia and Theta selected a tube on all trials. When the bait was located inside the bent tube, Heiji and Zilla failed to select a tube on 4 and 6 trials respectively despite searching in all the tubes repeatedly. Looking at only those trials on which a selection was made, Zilla, Heiji and Kiki selected the correct tube significantly above chance (33%) only when a straight tube was baited (straight tube baited: Heiji: 20/20, Kiki: 13/20 and Zilla: 18/20 correct, binomial tests: all $p<0.005$; bent tube baited- Heiji: 3/8, Kiki: 4/12 and Zilla: 2/6 correct, binomial tests: all $p>0.05$). Theta and Zinnia continued to show strong location biases against and for the middle tube (0 and 29 selections out of 32 respectively). The following analyses are again restricted to the three successful monkeys, assessed individually using non-parametric tests.

6.10.2. Search behaviour

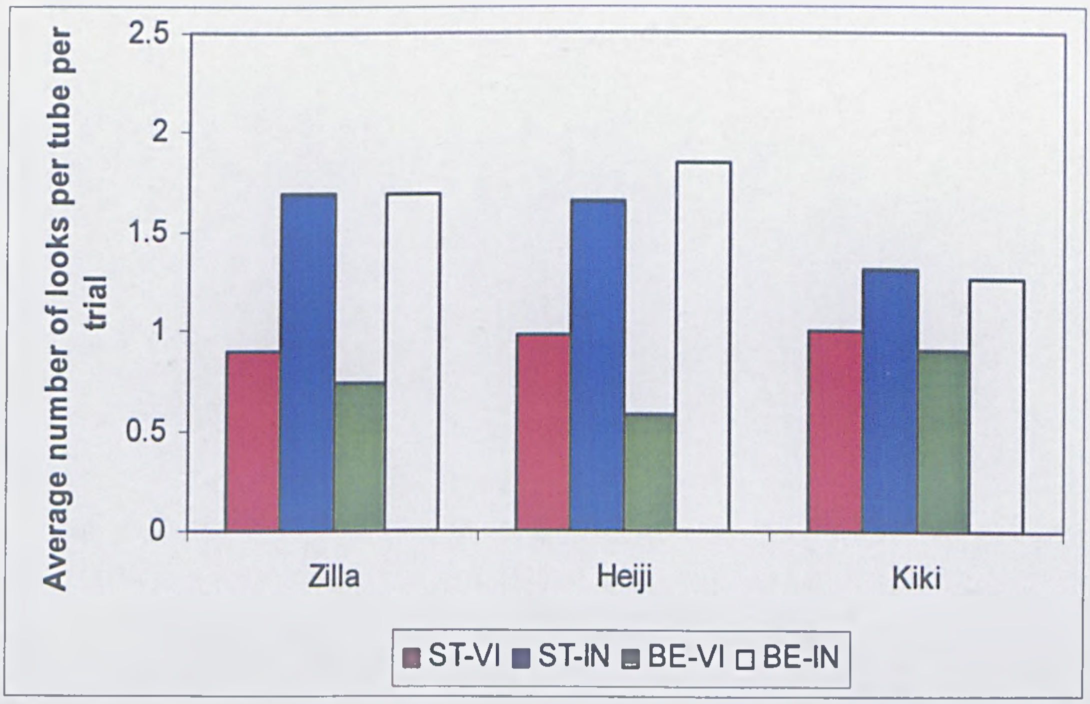

Figure 6.3: Experiment 2 - average number of looks per tube per trial according to baiting conditions. ST-VI: looks into straight tubes, bait in straight tube; BE-VI: looks into bent tube, bait in straight tube; ST-IN: looks into straight tubes, bait in bent tube; BE-IN: looks into bent tube, bait in bent tube.

Zilla, Heiji and Kiki looked into at least one tube on all trials. Figure 6.3 shows how the monkeys made significantly more looks in trials when the bait was in the bent tube compared to trials where the bait was in a straight tube, regardless of whether the trial ended with a correct or incorrect response (Mann-Whitney: Heiji: $z=-3.569$, $p<0.001$; Kiki: $z=-1.988$, $p=0.047$; Zilla: $z=-3.269$, $p<0.001$). Comparing the number of looks into straight tubes and the bent tube on each trial, the monkeys looked equally frequently into the bent tube and the straight tubes (adjusted for unequal number of tubes; Wilcoxon Signed Ranks Tests: Heiji: $z=-1.039$, Kiki: $z=-0.744$, Zilla: $z=-1.034$, all $p>0.05$). Finally, no successful 'super-efficient' searches (selecting the bent tube without searching it when the two straight tubes proved to be empty) occurred, although a total of 36 were possible for all three monkeys combined.

6.11. Discussion

The most significant finding from this study is that three monkeys completed Experiment 2 above chance, but only when the bait was placed inside a straight tube and therefore could be located through visual searching. When the bait was inside the bent tube and therefore not visible the monkeys continued searching, failed to make a selection on a total of 10 trials, and generally failed to predict the bait's location within the bent tube. This finding suggests that the monkeys may not have projected a goal state through secondary representations which could have guided their actions, and is in line with negative findings on invisible displacement tasks for capuchin monkeys (Natale & Antinucci, 1989).

The monkeys also did not avoid searching the bent tube, which may suggest that they failed to understand the visual affordances of the bent tube, i.e. that lines of sight must be straight. In humans, this ability appears to develop around 5 years of age. Flavell, Green, Herrera & Flavell (1991) showed young children tubes with different degrees of curvature, and asked them to predict whether they would be able to see objects placed at the other end of the tubes when looking through them. Over 70% of 3-year-old children, and 53% of the 5-year-olds believed they would be able to see the objects through a 90 degrees bent tube, failing to appreciate that lines of sight must be straight. The children were then allowed to test their predictions and to look through one of the tubes. After this feedback, the same tubes as in pre-feedback were shown to the children, who again were asked whether they would be able to see an object placed at the other end of the tubes. This time, 80% of the 5-year-olds gave the correct answer, but 68% of the 3-year-olds still failed.

Capuchin monkeys might similarly fail to realise that they cannot see around corners, despite receiving feedback about their search performance on every trial (when seeing or not seeing the bait in the bent tube). However, since the baiting was done invisibly, they could not know that the bait was only ever placed behind and not in front of the bend and therefore always hidden from view. Possibly with more trials the monkeys would have mastered this aspect of the experimental procedure. Only a small number of trials was conducted to test the monkeys' spontaneous understanding of their visual search behaviour and to exclude improved performance through simple associations. Future studies could usefully run more trials with bent tubes to assess eventual adaptation of the monkeys' understanding of their own search behaviour.

6.12. General Discussion and Conclusion: Do capuchin monkeys represent goal states of their actions?

In two experiments three out of five capuchin monkeys successfully obtained a food reward that was placed inside one of three tubes. In Experiment 1 these monkeys continued searching when they already knew (or should have known) that the bait was visible inside transparent tubes, and searching did not increase their success in obtaining the reward. In Experiment 2 when the bait was placed within a bent tube so that it could not be seen, the monkeys persistently searched in the bent tube, failing to show any understanding that they could not obtain information about the bait location from it. In both experiments the monkeys failed to predict the correct bait location from the information they obtained from the remaining tubes. That is, in Experiment 1, no instances of 'super-efficient' searches occurred; in Experiment 2, the monkeys selected tubes randomly when the bait was hidden inside the bent tube.

Failure to engage in 'super-efficient' searches and predicting the location of the reward contrasts with what could be expected in the presence of a projected goal state, which would allow the monkeys to follow a series of intermediate steps to achieve a final goal. Instead it appears that seeing the bait inside a tube eventually triggered the selection of that tube. This interpretation is supported by the fact that in Experiment 1 the majority of trials consisted of the monkeys looking into the baited tube immediately before making a selection, and the absence of any 'super-efficient' searches. Furthermore in Experiment 2, when the bait could not be seen, two otherwise successful monkeys failed to select a tube on a total of 10 occasions. Selection responses based on associations between searching and selection would suggest that in this instance capuchins were not using secondary representations to project a final goal state. However, given the small sample size and lack of varied age and sex classes, the present results should be regarded as preliminary and in need of replication.

It is also conceivable that the capuchin monkeys' excessive searching reflected an inability to inhibit previously learned behavioural sequences. Capuchin monkeys but not chimpanzees find it difficult to inhibit cursor movements directly toward the goal in mazes presented on a computer screen (Fragaszy et al., 2003). Difficulties with inhibiting learned behavioural sequences might have caused the two unsuccessful monkeys in the current study to develop strong location biases, and the three successful monkeys to unnecessarily search in the tubes. Capuchin monkeys are also known for their almost excessive curiosity and exploratory drive (Fragaszy et al., 2004), which may have further increased this species' likelihood of searching before making a selection. Future studies might increase the relative cost of searching by spacing the tubes further apart, or adjusting the height of tubes to make them more difficult to look into (Hampton et al., 2004) to help capuchin monkeys to control these potential difficulties.

It is noteworthy that a comparable failure to fully comprehend the consequences of actions has been described for capuchin monkeys' tool-use. Visalberghi & Limongelli (1996) reported that a capuchin monkey that used straw to dip for honey through holes in the side of a box persisted in trying to dip through the sides when the holes were moved to the top of the box. Fujita, Kuroshima & Asai (2003) found that capuchin monkeys are sensitive to the spatial arrangements of food and tools, but fail to take into account other environmental circumstances. Fragaszy et al. (2004) argued that even though capuchin monkeys are proficient tool users, they fail to understand the underlying causal relations between tools and objects and do not anticipate the outcomes of their manipulations. Capuchins may therefore generally fail to consider possible alternative future outcomes, which suggests a generalised failure to use secondary representations to project future goal states.

In conclusion, the presented experiments suggest that the capuchin monkeys were not planning their search behaviour and were not searching tubes with an explicitly represented goal in mind, which would require the use of secondary representations.

Others have linked performance on the tube task to meta-representational achievements, i.e. awareness of one's own knowledge states (Call & Carpenter, 2001; Call, 2003; Hampton et al., 2004). A meta-representational framework might be premature, however; one would need to distinguish between a metarepresentational interpretation ("I know the food must be at x") and a secondary goal-achievement interpretation ("the food must be at x"), which may be impossible based on behavioural observations alone (Browne, 2003). Clearly, if capuchins failed a task indicative of secondary representations, one would predict that they would also fail a task that is indicative of metarepresentations as metarepresentations are based on secondary representational abilities (Perner, 1991). However, as the presented experiments also contain some severe limitations (most notably the small sample size), further studies addressing these limitations appear highly desirable before further conclusions should be drawn.

Chapter Summary

Two experiments are reported in this chapter, which were aimed at investigating capuchin monkeys' ability to conceive of potential future goal states (using secondary representations) in a visual search task. Monkeys were presented with three tubes (one baited), and were required to select the baited tube. Results from both experiments showed that the monkeys were highly successful in selecting the correct tube when the bait could be seen through searching, yet their search patterns were mostly inefficient and no instances of inferring the bait location were observed. These results suggest that the monkeys did not base their search behaviour on a projected goal state, and are in line with an absence of secondary representational abilities.

Chapter 7: Secondary Representational Abilities in Monkeys – Evaluation and Future Directions

This final chapter draws together the results of the presented experimental work, and evaluates pig-tailed macaques' and capuchin monkeys' representational abilities based on the current results. An attempt is made to explore the potential causes for differential representational abilities in primates, and to further consider the implications of this difference in relation to the cognitive capacities of human and nonhuman apes. Future potential research directions are outlined, and the importance of research into representational abilities in nonhumans is discussed.

7.1. Representational abilities in humans and other primates

Chapter 1 set out with a definition of the concept of mental representations, and introduced the classification system of representational complexity by Perner (1991). Perner distinguished three types of representations: primary representations, which capture and represent reality faithfully and accurately; secondary representations, which are thought to be 'detached' from the immediate environment and therefore capable of mediating past, future, or entirely hypothetical situations; and metarepresentations, which explicitly represent the relation between the representation and the representational content. Numerous studies have provided supporting evidence for the development of this representational hierarchy in humans, with primary representations already present at birth (e.g. neonatal imitation; Meltzoff & Moore, 1977), secondary representations emerging around 1.5-2 years (e.g. mirror self-recognition; Amsterdam, 1972) and metarepresentations developing between 4-5 years (e.g. false belief; Wimmer & Perner, 1983).

Recently, comparative research efforts have sought evidence of similar representational complexity in other primates. Great apes (mostly based on evidence from chimpanzees) appear to hold primary representations (e.g. neonatal imitation; Myowa-Yamakoshi et al., 2004) as well as secondary representations (e.g. mirror self-recognition; Gallup, 1970). No strong supporting experimental evidence for the presence of metarepresentational abilities in apes has been obtained to date (e.g. failure to pass a false belief task; Call & Tomasello, 1999). Regarding monkeys, it appears that monkeys also hold at least primary representations (e.g. neonatal imitation; Ferrari et al., in prep), yet evidence for secondary representations is either weak (e.g. failure to self-recognise in a mirror; Anderson, 1984; some ambiguous results, e.g. Boccia, 1994) or relevant studies have not been conducted to date (e.g. no examination of attribution of emotions). Similarly, to date monkeys have not been tested for many metarepresentational achievements under controlled laboratory conditions. The current state of knowledge has led some to argue that secondary representational abilities are well-developed in great apes, but are absent in monkeys (Suddendorf, 1999).

This conclusion is based on studies that have comprised comparatively few subjects and normally of only one species. Given that there are over 150 recognised species of monkeys, it appears premature to presume that all monkeys of all species are incapable of holding secondary representations. The presented work was designed to further examine representational abilities in two monkey species in an attempt to outline both similarities and differences in representational abilities between monkeys and apes, thus potentially helping to trace the evolutionary origins of cognitive abilities in primates, including humans.

7.2. Examining the experimental evidence: Do pig-tailed macaques and capuchin monkeys have secondary representational abilities?

Three studies were conducted with pig-tailed macaques and three studies were conducted with capuchin monkeys, all aimed at revealing potential underlying secondary representational abilities. Pig-tailed macaques were tested for imitation, imitation recognition and mirror self-recognition (MSR); capuchins were tested for imitation recognition, MSR, and means-ends reasoning. Below, the results from the experimental chapters are briefly summarised (see also Table 7.1).

7.2.1. Pig-tailed macaques

In Chapter 2, macaques were trained to repeat self-directed behaviours following a neutral 'repeat' signal, which was argued to rely on primary representational abilities. Further tests regarding multiple mnemonic aspects and transfer to novel behaviours largely confirmed the presence of primary representations. It was argued that success on a n-back version of this task requires secondary representations, yet when attempted to test for long-term recall of the target behaviour (a necessary requirement for the n-back version), the monkeys did not respond significantly above chance levels. Hence in Chapter 2 the monkeys did not show any evidence for secondary representational abilities.

Chapter 3 examined whether macaques recognise when they themselves are being imitated. It was argued that visual discrimination between an imitator and a non-imitator is indicative of primary representations, and that secondary representations can be inferred if the monkeys show instances of contingency testing behaviours. The macaques looked significantly longer at the imitator compared to the non-imitator, thereby confirming their primary representational abilities. However, no contingency testing behaviours were observed. Hence, Chapter 3 also failed to provide any evidence for secondary representational abilities in pig-tailed macaques.

Chapter 4 described a formal mark test with the same pig-tailed macaques, hypothesising that evidence for primary representation might correlate with evidence for secondary representations. Even though no strong evidence for self-recognition was found during the mark test, the same monkeys that showed strong indicators for imitation recognition were observed to touch the marked areas on their heads. This result suggests a connection between primary and secondary representational abilities within the same individuals, yet no conclusive evidence for secondary representations was found.

7.2.2. Capuchin monkeys

Chapter 3 also reported the results of an imitation recognition experiment with a group of capuchin monkeys. The capuchins discriminated between an imitator and a non-imitator of their actions as shown by a significant visual preference for the non-imitator, which indicates at least primary representational abilities. No instances of contingency testing behaviours were observed, which suggests an absence of secondary representational abilities.

In Chapter 5 a new manipulation was intended to overcome a previous limitation of classic MSR studies. It was hypothesised that additional mirror image stimulation in the form of two simultaneous mirror objects might promote MSR in capuchins. In addition, the mirrors were altered in either their physical complexity or image quality in order to investigate which factors inherent to the mirror object might be particularly suitable for eliciting MSR. The results of this study suggest that the physical complexity of the mirror objects did not affect the monkeys' interactions with the mirrors, but that the monkeys showed more interest in clearly discernable reflections. No evidence of MSR and therefore secondary representational abilities was found.

Finally, Chapter 6 tested capuchin monkeys on a means-ends visual search task, which was thought to rely on their ability to use secondary representations to conceive of potential future goal states. It was found that although the monkeys could successfully retrieve a food reward from a hiding place, the inefficiency of their visual search patterns suggested that they did not base their searches on a projected goal state. Hence, these experiments also failed to find any evidence for secondary representational abilities in capuchin monkeys.

7.3. Evaluation and limitations of the experimental evidence

The experimental data provided supporting evidence for primary representational abilities in both species, which is in line with evidence of primary representational achievements from previous studies (see also Table 7.1.). Failure to find evidence for secondary representational abilities also confirms previous failures to obtain any positive evidence for both species. These converging data might suggest a true

Table 7.1. Evidence for representational complexity in *Macaca nemestrina* and *Cebus apella*. Orange shaded portions represent work from the present thesis. *=no reports or assessments of this ability are found in the literature for either species.

		Study	**Species**	**Evidence?**
Primary Representation	Neonatal Imitation	Ferrari (personal communication, 2004)	Macaca nemestrina	YES
	Visible Displacement	Dumas & Brunet, 1994	Cebus apella	YES
	Kinaesthetic-visual matching	Chapter 2 (self-imitation)	Macaca nemestrina	YES
		Chapter 3 (imitation recognition – visual discrimination)	Macaca nemestrina	YES
		Chapter 3 (imitation recognition – visual discrimination)	Cebus apella	YES
Secondary Representation	Pretend Play	?*	?*	?*
	Invisible displacement	Dumas & Brunet, 1994	Cebus apella	NO
	Means-ends reasoning	Visalberghi & Limongelli, 1994	Cebus apella	NO
		Chapter 6 (visual search task)	Cebus apella	NO
	Understand external representations	?*	?*	?*
	Mirror self-recognition	Thompson & Boatright-Horowitz, 1994	Macaca nemestrina	AMBIGUOUS
		Boccia, 1994	Macaca nemestrina	AMBIGUOUS
		Chapter 4 (MSR)	Macaca nemestrina	AMBIGUOUS
		Lethmate & Ducker, 1973	Cebus apella	NO
		Marchal & Anderson, 1993	Cebus apella	NO
		Riviello et al., 1992	Cebus apella	NO
		Anderson & Roeder, 1989	Cebus apella	NO
		De Waal et al., 2005	Cebus apella	NO
		Chapter 5 (MSR)	Cebus apella	NO
	Attribute intentions and emotions	Chapter 3 (imitation recognition - contingency testing behaviours)	Macaca nemestrina	NO
		Chapter 3 (imitation recognition - contingency testing behaviours)	Cebus apella	NO
	Generalised imitation	Mitchell & Anderson, 1993	Macaca nemestrina	NO
		Chapter 2 (n-back self-imitation)	Macaca nemestrina	NO
		Visalberghi & Fragaszy, 2002	Cebus apella	NO

absence of secondary representations, however any such negative conclusion should be regarded with caution. For example, it is conceivable that secondary representations are an advanced cognitive ability that may not be present in the entire subject population. Since the presented data as well as previous studies were based on small sample sizes, replications of the present procedures with larger sample sizes may find positive evidence.

Table 7.1 summarises selected available evidence concerning representational complexity for pig-tailed macaques and capuchin monkeys. It should be noted that several behaviours indicative of secondary representations have not been systematically tested in either one species (e.g. invisible displacement and means-ends reasoning for pig-tailed macaques) or both species (e.g. understanding of external representations). One might argue that the absence of secondary representations in one area should indicate absence of secondary representations in other areas, since a general absence of secondary representational abilities would lead to negative results in all areas. However, it is possible that some behaviours rely on secondary representations more than others, or on different types of secondary representations (e.g. past and future content). For example, Asendorpf et al. (1996) found that infants who recognised intentional imitation nonetheless produced (false) negatives on a subsequent mark test. Therefore, it remains possible that future research might discover positive evidence in both pig-tailed macaques and capuchin monkeys in other areas relying on secondary representational abilities. It is also recommended that future studies investigate representational abilities within rather than across individuals, which would help in identifying the pattern in which behaviours indicative of secondary representations emerge.

Despite the failure to find strong evidence for secondary representations, pig-tailed macaques have now shown ambiguous responses to a mark test in three studies (Thompson & Boatright-Horowitz, 1994; Boccia, 1994; present data, Chapter 4). This finding stands out from all the other mark tests conducted with monkeys in that different pig-tailed macaques repeatedly showed responses to the marks on their heads. All studies reported that responses were not accompanied by close visual monitoring via the mirror (as can be observed in apes) but instead consisted of swipes of the hand across the face. Therefore, the results cannot be regarded as conclusive evidence for MSR. Nonetheless, it is intriguing that this species (unlike all the other monkey species tested to date) appears to respond to the marks.

It is not clear to what cause this mark-directed behaviour can be attributed. As argued in Chapter 1, one reason might be that an evolutionary ancestor of both monkeys and apes first developed the capacity for secondary representational abilities, which then continued to be passed down through generations. This explanation fits well with the present data in that pig-tailed macaques (an Old World species and thus more closely related to humans than New World species) showed such responses, but no similar evidence has ever been reported for capuchin monkeys (a New World species). However, this argument by homology does not explain why pig-tailed macaques and no other Old World species should have retained this trait. Furthermore, it was argued in Chapter 1 that ecological pressures may have led to advanced representational abilities. Both pig-tailed macaques and capuchin monkeys appear to face similar social pressures, but capuchin monkeys feed on more difficult-to-obtain food items compared to pig-tailed macaques, and this kind of extractive foraging may give rise to a greater need for advanced representational abilities. Hence, if ecological pressures have led to secondary representations, it would be expected that capuchin monkeys rather than pig-tailed macaques would show evidence for secondary representations. Neither the argument by homology nor ecological pressures thus appear to sufficiently explain pig-tailed macaques' ambiguous mark test responses.

One potentially critical factor that has been neglected in the present experiments is the subjects' social rearing history. Early rearing experiences have a profound impact on individuals' cognitive and behavioural development. Some have even argued that close human contact early in life may lead to new cognitive abilities that animals would otherwise not develop (also called enculturation; e.g. Tomasello, Kruger & Ratner, 1993). Bard & Gardner (1996) demonstrated experimentally that different rearing practices can significantly affect chimpanzees' development. Bard & Gardner (1996) measured cognitive development and personality expressions in three different groups of chimpanzee infants. Group 1 (infants whose mothers did not care sufficiently for them) underwent standard laboratory care, consisting of peer-group contact and regulated feeding and cleaning. Group 2, called the responsive care group, was also reared with same-age peers, but received daily physical contact with human carers in the form of play sessions. Group 2 received feeding when required, and was eased into any significant changes in care circumstances. Group 3 consisted of infants whose mothers initially looked after them, but later on failed to provide adequate care. These 'late arrivals' thus had normal mother-rearing experiences before undergoing standard laboratory care. Bard and Gardner found few differences in cognitive abilities between the groups (using e.g. the Bayley Scales of Infant Development), but that responsive care infants scored marginally higher on cognitive assessment scales. Responsive care infants were also rated to show higher levels of happiness and more co-operation with the behavioural assessments. In addition to their relevance to the enculturation hypothesis, these findings indicate that performance on cognitive tasks may be affected by individuals' rearing experiences and the amount of exposure to human contact. Unfortunately, the rearing history of the study animals of the present work is largely unknown, but it appears unlikely that the pig-tailed macaques in all three ambiguous mark test studies were reared in similar responsive care arrangements that caused improved performance on the mark test. However, rearing experiences should be considered in future work in this area as an important contributing factor to cognitive performances.

7.4. Future research directions

To date, there is no satisfactory explanation for pig-tailed macaques' mark test responses. Clearly this phenomenon is in need of further investigation, which should also help us to better understand the evolutionary origins of representational complexity in great apes and humans. Although the development of representational abilities is well documented in human infants, virtually nothing is known about the ontogenetic development of representational abilities in apes and monkeys. Some attempts have been made to trace the emergence of MSR in chimpanzees, with conflicting results (e.g. compare Lin et al., 1992 with Povinelli et al., 1993). Mapping out the ontogenetic development would not only help to refine current research efforts e.g. by targeting only appropriate age groups, but would also allow us to directly compare age-related representational achievements across species.

Bearing in mind these additional factors, future research should address the remaining 'blanks' in secondary representational achievements of monkeys.
In this context, better results might be achieved if the behaviour indicative of secondary representations is a necessary element of the task itself rather than a by-product. For example in the imitation recognition task (Chapter 3), contingency testing behaviours (which are thought to rely on secondary representations) were at no point necessary for task performance. Hence, their absence might simply represent a sampling error, and future tasks relying on their occurrence might find positive evidence (similar arguments can be made with regard to experiments in Chapters 4-6). Furthermore, researchers should consider testing animals under more ecologically relevant conditions rather than approaching comparative research from a human perspective. Poss & Rochat (2003) showed that when children are put in unfamiliar non-verbal contexts, they perform worse than apes on cognitive tasks (who are used to non-verbalised task requirements). In other words, better overall results may be obtained if the animals are tested in appropriate, species-specific contexts. Taking into account these recommendations, future research on representational complexity in nonhuman primates has still much to contribute to our understanding of human and nonhuman cognition.

References

Agnetta, B., & Rochat, P. (2004). Imitative games by 9-, 14-, and 18-month-old infants. *Infancy, 6*, 1-36.

Amsterdam, B. (1972). Mirror self-image reactions before age two. *Developmental-Psychobiology,* 5, 297-305.

Anderson, J. R. (1983). Mirror-image stimulation and short separations in stumptail monkeys. *Animal Learning and Behavior, 11*, 139-143.

Anderson, J. R. (1984). Monkeys with mirrors: some questions for primate psychology. *International Journal of Primatology, 5*, 81-98.

Anderson, J. R. (1984). The development of self-recognition: A review. *Developmental-Psychobiology, 17*, 35-49.

Anderson, J. R. (1986). Mirror-mediated finding of hidden food by monkeys (Macaca tonkeana and M. fascicularis). *Journal of Comparative Psychology, 100*, 237-242.

Anderson, J. R. (1993). To see ourselves as others see us: A response to Mitchell. *New Ideas in Psychology, 11*, 339-346.

Anderson, J. R. (1994). The monkey in the mirror: A strange conspecific. In: Parker, S. T., Mitchell, R. W. & Boccia, M. L. (Eds), *Self-awareness in animals and humans: Developmental perspectives.* (pp.315-329). New York: Cambridge University Press.

Anderson, J. R., Fritsch, C., & Favre, B. (1990). Operant conditioning of scratching in lemurs. *Primates, 31*, 611-615.

Anderson, J. R., & Gallup, G. G. Jr. (1997). Self-recognition in Saguinus? A critical essay. *Animal Behaviour, 54*, 1563-1567.

Anderson, J. R., & Gallup, G. G. Jr. (1999). Self-recognition in nonhuman primates: Past and future challenges. In: Whalen, R. E. & Haug, M. (eds), *Animal models of human emotion and cognition.* (pp.175-194). Washington: American Psychological Association.

Anderson, J. R., & Roeder, J. J. (1989). Responses of capuchin monkeys (Cebus apella) to different conditions of mirror-image stimulation. *Primates, 30*, 581-587.

Anisfeld, M. (1996). Only tongue protrusion modeling is matched by neonates. *Developmental Review, 16*, 149-161.

Anisfeld, M., Turkewitz, G., Rose, S. A., Rosenberg, F. R., Sheiber, F. J., & Couturier Fagan, D. A. (2001). No compelling evidence that newborns imitate oral gestures. *Infancy, 2*, 111-122.

Armstrong, D. (1968). *A Materialist Theory of the Mind.* London: Routledge.

Asendorpf, J. B., & Baudonniere, P. M. (1993). Self-awareness and other-awareness: Mirror self-recognition and synchronic imitation among unfamiliar peers. *Developmental Psychology, 29*, 88-95.

Asendorpf, J. B., Warkentin, V., & Baudonniere, P. M. (1996). Self-awareness and other-awareness II: Mirror self-recognition, social contingency awareness, and synchronic imitation. *Developmental Psychology, 32*, 313-321.

Astington, J. W. (1993). *The child's discovery of the mind.* London: Fontana Press.

Astington, J. W., & Gopnik, A. (1991). Developing understanding of desire and intention. In: Whiten, A. (Ed), *Natural theories of mind: Evolution, development and simulation of everyday mindreading.* (pp. 39-50). Oxford: Blackwell.

Astington, J. W., & Jenkins, J. M. (1999). A longitudinal study of the relation between language and theory-of-mind development . *Developmental-Psychology, 35*, 1311-1320.

Aureli, F.E., & de Waal, F. B. M. (2000). *Natural conflict resolution.* Berkeley: University of California Press.

Baddeley, A. (2001). The concept of episodic memory. *Philosophical Transactions of the Royal Society London B, 356*, 1345-1350.

Bard, K. A., Fragaszy, D. M., & Visalberghi, E. (1995). Acquisition and comprehension of a tool-using behavior by young chimpanzees (Pan troglodytes): Effects of age and modeling. *International Journal of Comparative Psychology, 8*, 47-68.

Bard, K. A., & Gardner, K. H. (1996). Influences on development in infant chimpanzees: Enculturation, temperament, and cognition. In: Russon, A. E., Bard, K. A., & Parker, S. T. (eds), *Reaching into thought: the minds of the great apes.* (pp. 235-256). New York: Cambridge University Press.

Bard, K. A., & Russell, C. L. (1999). Evolutionary foundations of imitation: Social cognitive and developmental aspects of imitative processes in non-human primates. In: Butterworth, G., & Nadel, J. (eds), *Imitation in infancy.* (pp.89-123). New York: Cambridge University Press.

Baron-Cohen, S., Leslie, A. M., & Frith, U. (1985). Does the autistic child have a "theory of mind"? *Cognition, 21,* 37-46.

Bauer, P. J., Schwade, J. A., Wewerka, S. S., & Delaney, K. (1999). Planning ahead: Goal-directed problem solving by 2-year-olds. *Developmental Psychology, 35,* 1321-1337.

Beck, B. B. (1980). *Animal Tool Behavior.* Garland STPM Press.

Benhar, E., Carlton, P. L., & Samuel, D. (1974). A search for mirror-image reinforcement and self-recognition in the baboon. *Contemporary Primatology,* 202-208.

Bering, J. M., Bjorklund, D. F., & Ragan, P. (2000). Deferred imitation of object-related actions in human-reared juvenile chimpanzees and orangutans. *Developmental Psychobiology, 36,* 218-232.

Berk, L. E. (2000). *Child development* (5th Ed.). London: Allyn and Bacon.

Bird, L. R., Roberts, W. A., Abroms, B., Kit, A. A., & Crupi, C. (2003). Spatial memory for food hidden by rats (Rattus norvegicus) on the radial maze: studies of memory for where, what, and when. *Journal of Comparative Psychology, 117,* 176-187.

Bjorklund, D. F., Bering, J. M., & Ragan, P. (2000). A two-year longitudinal study of deferred imitation of object manipulation in a juvenile chimpanzee (Pan troglodytes) and orangutan (Pongo pygmaeus). *Developmental Psychobiology, 37*, 229-237.

Bjorklund, D. F., Yunger, J. L., Bering, J. M., & Ragan, P. (2002). The generalization of deferred imitation in enculturated chimpanzees (Pan troglodytes). *Animal Cognition, 5*, 49-58.

Boccia, M. L. (1994). Mirror behavior in macaques. In:. Parker, S. T., Mitchell, R. W., & Boccia, M. L. (eds), *Self-awareness in animals and humans: Developmental perspectives.* (pp.350-360). New York: Cambridge University Press.

Boesch, C., & Boesch, H. (1983). Optimisation of nut-cracking with natural hammers by wild chimpanzees. *Behaviour, 83*, 265-286.

Boesch, C., & Boesch, H. (1984). Mental map in wild chimpanzees: An analysis of hammer transports for nut cracking. *Primates, 25*, 160-170.

Boesch, C., & Boesch, H. (1990). Tool use and tool making in wild chimpanzees. *Folia Primatologica, 54*, 86-99.

Bovet, D., & Vauclair, J. (1998). Functional categorization of objects and of their pictures in baboons (Papio anubis). *Learning and Motivation, 29*, 309-322.

Bower, T. (1974). *Development in infancy.* Oxford: W. H. Freeman.

Boysen, S., & Berntson, G. (1995). Responses to quantity: perceptual versus cognitive mechanisms in chimpanzees (Pan troglodytes). *Journal of Experimental*

Psychology: Animal Behavior Processes, 21, 82-86.

Bradshaw, R. H. (1998). Consciousness in non-human animals: Adopting the precautionary principle. *Journal of Consciousness Studies, 5*, 108-114.

Brewer, S. M., & McGrew, W. (1990). Chimpanzee use of a tool-set to get honey. *Folia Primatologica, 54*, 100-104.

Browne, D. (2003). Some sceptical thoughts about metacognition. *Behavioral and Brain Sciences, 26*, 340-341.

Bullock, M., & Lutkenhaus, P. (1988). The development of volitional behavior in the toddler years. *Child Development, 59*, 664-674.

Byrne, R. W. (1993). The meaning of "awareness": A response to Mitchell. *New Ideas in Psychology, 11*, 347-350.

Byrne, R. W., & Whiten, A. (1988). *Machiavellian intelligence: Social expertise and the evolution of intellect in monkeys, apes, and humans.* New York: Clarendon Press.

Caldecott, J. O. (1986). Mating patterns, societies and the ecogeography of macaques. *Animal Behaviour, 34*, 208-220.

Call, J. (2001). Object permanence in orangutans (Pongo pygmaeus), chimpanzees (Pan troglodytes), and children (Homo sapiens). *Journal of Comparative Psychology, 115*, 159-171.

Call, J. (2003). Beyond learning fixed rules and social cues: abstraction in the social arena. *Philosophical Transaction of the Royal Society of London B, 358*, 1189-1196.

Call, J., & Carpenter, M. (2001). Do apes and children know what they have seen? *Animal Cognition, 3,* 207-220.

Call, J., & Tomasello, M. (1998). Distinguishing intentional from accidental actions in orangutans (Pongo pygmaeus), chimpanzees (Pan troglodytes) and human children (Homo sapiens). *Journal of Comparative Psychology, 112*, 192-206.

Call, J., & Tomasello, M. (1999). A nonverbal false belief task: The performance of children and great apes. *Child Development, 70,* 381-395.

Clayton, N. S., & Dickinson, A. (1998). Episodic-like memory during cache recovery by scrub jays. *Nature, 395*, 272-274.

Cleveland, A., Rocca, A. M., Wendt, E. L., & Westergaard, G. C. (2004). Transport of tools to food sites in tufted capuchin monkeys (Cebus apella). *Animal Cognition, 7*, 193-198.

Collinge, N. E. (1989). Mirror reactions in a zoo colony of *Cebus* monkeys. *Zoo Biology, 8,* 89-98.

Conway, M., Campbell, R., & Gathercole, S. (2001). Introduction: case studies in the neuropsychology of memory. In: Campbell, R., & Conway. M. A. (eds), *Broken memories: case studies in memory impairment* (pp. i-xxvi). Cambridge: Blackwell.

Corrigan, R. (1987). A developmental sequence of actor-object pretend play in young children. *Merrill Palmer Quarterly, 33*, 87-106.

Custance, D. M., & Bard, K. A. (1994). The comparative and developmental study of self-recognition and imitation: The importance of social factors. In: Parker, S. T., Mitchell, R. W., & Boccia, M. L. (eds), *Self-awareness in animals and humans: Developmental perspectives.* (pp.207-226). New York: Cambridge University Press.

Custance, D. M., Whiten, A., & Bard, K. A. (1995). Can young chimpanzees (Pan troglodytes) imitate arbitrary actions? Hayes & Hayes (1952) revisited. *Behaviour, 132*, 837-859.

Davenport, R. (1976). Cross-modal perception in apes. *Annals New York Academy of Sciences, 280*, 143-149.

Dawkins, M. S. (2001). Who needs consciousness? *Animal Welfare, 10,* S19-S29.

Dawson, G., & McKissick, F. C. (1984). Self-recognition in autistic children. *Journal of Autism and Developmental Disorders, 14,* 383-394.

de Blois, S. T., & Novak, M. A. (1994). Object permanence in rhesus monkeys (Macaca mulatta). *Journal of Comparative Psychology, 108*, 318-327.

de Blois, S. T., Novak, M. A., & Bond, M. (1998). Object permanence in orangutans (Pongo pygmaeus) and squirrel monkeys (Saimiri sciureus). *Journal of Comparative Psychology, 112*, 137-152.

de Lannoy, J. (1993). Two theories of a mental model for mirror-self-recognition: A response to Mitchell. *New Ideas in Psychology, 11,* 337-338.

de Lillo, C., Aversano, M., Tuci, E., & Visalberghi, E. (1998). Spatial constraints and regulatory functions in monkeys' (Cebus apella) search. *Journal of Comparative Psychology, 112*, 353-362.

de Lillo, C., Visalberghi, E., & Aversano, M. (1997). The organization of exhaustive searches in a patchy space by capuchin monkeys (Cebus apella). *Journal of Comparative Psychology, 111*, 82-90.

de Moura, A., & Lee, P. C. (2004). Capuchin stone tool use in Caatinga dry forest. *Science, 306*, 1909.

de Veer, M. W., Gallup, G. G. Jr., Theall, L. A., van den Bos, R., & Povinelli, D. J. (2003). An 8-year longitudinal study of mirror self-recognition in chimpanzees (Pan troglodytes). *Neuropsychologia, 41*, 229-234.

de Waal, F. B. M., & Aureli, F. E. (1996). Consolation, reconciliation, and a possible cognitive difference between macaques and chimpanzees. In: Russon, A., Bard, K. A., & Parker, S. T. (eds), *Reaching into thought: the minds of the great apes.* (pp.80-110). New York: Cambridge University Press.

de Waal, F. B. M., Dindo, M., Freeman, C., & Hall, M. (2005). The monkey in the mirror: Hardly a stranger. *Proceedings of the National Academy of Sciences, 102*, 11140-11147.

DeLoache, J. S. (1987). Rapid change in the symbolic functioning of very young children. *Science, 238*, 1556-1557.

DeLoache, J. S. (1991). Symbolic functioning in very young children: Understanding of pictures and models. *Child Development, 62*, 736-752.

Dennett, D. C. (1978). *Brainstorms*. London: Penguin Books.

Dennett, D. C. (1996). *Kinds of minds: Toward an understanding of consciousness*. New York: Basic Book.

Desmond, A. (1979). *The ape's reflection*. London: Blond & Briggs.

Diamond, A. (1991). Neuropsychological insights into the meaning of object concept development . In: Gelman, R., & Carey, S. (eds), *The epigenesis of mind: Essays on biology and cognition.* (pp.67-110). Hillsdale: Lawrence Erlbaum Associates.

Dienes, Z., & Perner, J. (1999). A theory of implicit and explicit knowledge. *Behavioral and Brain Sciences, 22*, 735-808.

Dirks, J., & Gibson, E. (1977). Infants' perception of similarity between live people and their photographs. *Child Development, 48*, 124-130.

Dumas, C., & Brunet, C. (1994). Object permanence in Capuchin monkeys: A study of invisible displacements / Permanence de l'objet chez le singe capucin (Cebus apella): etude des deplacements invisibles. *Canadian Journal of Experimental Psychology, 48*, 341-358.

Dunbar, R. I. (2000). Causal reasoning, mental rehearsal, and the evolution of primate cognition. In: Huber, L., & Heyes, C. (eds), *The evolution of cognition*. (pp.205-219). Cambridge: MIT Press.

Dunbar, R. I., McAdam, M. R., & O'Connell, S. (2005). Mental rehearsal in great apes (Pan troglodytes and Pongo pygmaeus) and children. *Behavioral Processes, 69,* 323-330.

Eysenck, M. W., & Keane, M. T. (2000). *Cognitive psychology: A student's handbook (4th Ed.).* New York: Psychology Press.

Fabricius, W. V. (1988). The development of forward search planning in preschoolers. *Child Development, 59,* 1473-1488.

Fagot, J., Martin-Malivel, J., & Depy, D. (2000). What is the evidence for an equivalence between objects and pictures in birds and nonhuman primates? In: Fagot, J. (Ed), *Picture perception in animals.* (pp.295-320). New York: Psychology Press.

Ferrari, P. F., Gallese, V., Rizzolatti, G., & Fogassi, L. (2003). Mirror neurons responding to the observation of ingestive and communicative mouth actions in the monkey ventral premotor cortex. *European Journal of Neuroscience, 17,* 1703-1714.

Ferrari, P. F., Visalberghi, E., Paukner, A., Fogassi, L., Ruggiero, A., & Suomi, S. (in prep). Behavioral responses to facial and hand gestures in infant rhesus macaques (Macaca mulatta).

Fillion, C., Washburn, D., & Gulledge, J. (1996). Can monkeys (Macaca mulatta) represent invisible displacement? *Journal of Comparative Psychology, 110,* 386-395.

Flavell, J. H., Flavell, E. R., & Green, F. L. (1983). Development of the appearance-reality distinction. *Cognitive Psychology, 15,* 95-120.

Flavell, J. H., Green, F. L., Herrera, C., & Flavell, E. R. (1991). Young children's knowledge about visual perception: Lines of sight must be straight. *British Journal* *of Developmental Psychology, 9*, 73-87.

Fragaszy, D. M., & Adams Curtis, L. E. (1991). Generative aspects of manipulation in tufted capuchin monkeys (Cebus apella). *Journal of Comparative Psychology, 105*, 387-397.

Fragaszy, D. M., Izar, P., Visalberghi, E., Ottoni, E., & de Oliveira, M. (2004). Wild capuchin monkeys (Cebus libidinosus) use anvils and stone pounding tools. *American Journal of Primatology, 64*, 359-366.

Fragaszy, D. M., Johnson Pynn, J., Hirsh, E., & Brakke, K. (2003). Strategic navigation of two-dimensional alley mazes: Comparing capuchin monkeys and chimpanzees. *Animal Cognition, 6*, 149-160.

Fragaszy, D. M., Visalberghi, E., & Fedigan, L. (2004). *The complete capuchin.* Cambridge: Cambridge University Press.

Fritz, J., Mortimer, M., & Saunders, R. (2005). In search of an auditory engram. *Proceedings of the National Academy of Sciences, 102*, 9359-9364.

Fujita, K., Kuroshima, H., & Asai, S. (2003). How do tufted capuchin monkeys (Cebus apella) understand causality involved in tool use? *Journal of Experimental Psychology: Animal Behavior Processes, 29*, 233-242.

Gaerdenfors, P. (1996). Cued and detached representations in animal cognition. *Behavioural Processes, 35*, 263-273.

Galef, B. J. (1990). Traditions in animals: field observations and laboratory analyses. In:

Bekoff, M., & Jamieson, D. (eds), *Methods, inference, interpretation and explanation of the study of behavior.* (pp.74-95). Boulder: Westview Press.

Galef, B. J. (1992). The question of animal culture. *Human Nature, 3*, 157-178.

Gallese, V., Ferrari, P. F., Kohler, E., & Fogassi, L. (2002). The eyes, the hand, and the mind: Behavioral and neurophysiological aspects of social cognition. In: Bekoff, M., Allen, C., & Burghardt, G. M. (eds), *The cognitive animal: Empirical and theoretical perspectives on animal cognition.* (pp.451-461). Cambridge: MIT Press.

Galloway, A. T., Addessi, E., Fragaszy, D. M., & Visalberghi, E. (2005). Social facilitation of eating familiar food in tufted capuchins (Cebus apella): Does it involve behavioral coordination? *International Journal of Primatology, 26*, 181-189.

Gallup, G. G. Jr. (1970). Chimpanzees: Self-recognition. *Science, 167*, 86-87.

Gallup, G. G. Jr. (1977). Absence of self-recognition in a monkey (Macaca fascicularis) following prolonged exposure to a mirror. *Developmental Psychobiology, 10*, 281-284.

Gallup, G. G. Jr. (1991). Toward a comparative psychology of self-awareness: species limitations and cognitive consequences. In: Goethals, G. R., & Strauss, J. (eds), *The self: an interdisciplinary approach.* (pp.121-135). New York: Springer Verlag.

Gallup, G. G. Jr. (1994). Self-recognition: Research strategies and experimental design. In: Parker, S. T., Mitchell, R. W., & Boccia, M. L. (eds), *Self-awareness in animals and humans: Developmental perspectives.* (pp.35-50). New York: Cambridge

University Press.

Gallup, G. G. Jr., & Povinelli, D. J. (1993). Mirror, mirror on the wall which is the most heuristic theory of them all? A response to Mitchell. *New Ideas in Psychology, 11,* 327-335.

Gallup, G. G. Jr., Povinelli, D. J., Suarez, S. D., Anderson, J. R., Lethmate, J., & Menzel, E. W. Jr. (1995). Further reflections on self-recognition in primates. *Animal Behaviour, 50*, 1525-1532.

Gallup, G. G. Jr., Wallnau, L., & Suarez, S. (1980). Failure to find self-recognition in mother-infant and infant-infant rhesus monkey pairs. *Folia Primatologica, 33*, 210-219.

Gergely, G. (1994). From self-recognition to theory of mind. In: Parker, S. T., Mitchell, R. W., & Boccia, M. L. (eds), *Self-awareness in animals and humans: Developmental perspectives*. (pp.51-60). New York: Cambridge University Press.

Gibson, K. (1986). Cognition, brain size and the extraction of embedded food resources. In: Else, J. G., & Lee, P. C. (eds), *Primate ontogeny, cognition and social behaviour.* (pp.93-103). Cambridge: Cambridge University Press.

Goodall, J. (1986). Social rejection, exclusion, and shunning among the Gombe chimpanzees. *Ethology and Sociobiology, 7*, 227-236.

Grether, W., & Maslow, A. (1937). An experimental study of insight in monkeys. *Journal of Comparative Psychology, 24,* 127-134.

Haake, R. J., & Somerville, S. C. (1985). Development of logical search skills in infancy. *Developmental Psychology, 21*, 176-186.

Hall, K. (1962). Behaviour of monkeys towards mirrors. *Nature, 196*, 1258-1261.

Hampton, R. R. (2001). Rhesus monkeys know when they remember. *Proceedings of the National Academy of Sciences, 98*, 5359-5362.

Hampton, R. R., Hampstead, B. M., & Murray, E. A. (2005). Rhesus monkeys (Macaca mulatta) demonstrate robust memory for what and where, but not when, in an open-field test of memory. *Learning and Motivation, 36,* 245-259.

Hampton, R. R., & Schwartz, B. L. (2004). Episodic memory in nonhumans: What, and where, is when? *Current Opinion in Neurobiology, 14,* 192-197.

Hampton, R. R., Zivin, A., & Murray, E. A. (2004). Rhesus monkeys (Macaca mulatta) discriminate between knowing and not knowing and collect information as needed before acting. *Animal Cognition, 7*, 239-246 .

Harris, H., & Edwards, A. (2004). Mirrors as environmental enrichment for African green monkeys. *American Journal of Primatology, 64*, 459-467.

Hauser, M. (2001). *Wild Minds*. London: Penguin Books.

Hauser, M. D., Kralik, J., Botto-Mahan, C., Garrett, M. & Oser, J. (1995). Self-recognition in primates: phylogeny and the salience of species-specific features. *Proceedings of the National Academy of Sciences, 92*, 10811-10814.

Hauser, M., Miller, C., Liu, K., & Gupta, R. (2001). Cotton-top tamarins (Saguinus oedipus) fail to show mirror-guided self-exploration. *American Journal of Primatology, 53*, 131-137.

Hayes, C. (1951). *The ape in our house.* Oxford: Harper.

Hayes, K. J., & Hayes, C. (1952). Imitation in a home-raised chimpanzee. *Journal of Comparative and Physiological Psychology, 45,* 450-459.

Herman, L. M. (2002). Vocal, social, and self-imitation by bottlenosed dolphins. In: Dautenhahn, K., & Nehaniv, C. L. (eds), *Imitation in animals and artifacts.* (pp.63-108). Cambridge: MIT Press.

Herman, L. M., Pack, A. A., & Morrel-Samuels, P. (1993). Representational and conceptual skills of dolphins. In: Roitblat, H. R., Herman, L. M., & Nachtigall, P. (eds), *Language and communication: Comparative perspectives.* (pp.403-442). Hillsdale: Lawrence Erlbaum Associates.

Heyes, C. M. (1994). Reflections on self-recognition in primates. *Animal Behaviour, 47,* 909- 919.

Hofstadter, M., & Reznick, J. (1996). Response modality affects human infant delayed-response performance. *Child Development, 67*, 646-658.

Howes, C., & Matheson, C. C. (1992). Sequences in the development of competent play with peers: Social and social pretend play. *Developmental Psychology, 28*, 961-974.

Humphrey, N. (1976). The social function of intellect. In: Bates, P. P. G., & Hinde, R.A. (eds), *Growing points in ethology.* (pp.303-317). Oxford: Cambridge University

Press.

Humphrey, N. (2002). *The mind made flesh.* Oxford: Oxford University Press.

Hyatt, C. W. (1998). Responses of gibbons (Hylobates lar) to their mirror images. *American Journal of Primatology, 45*, 307-311.

Itakura, S. (1987). Use of a mirror to direct their responses in Japanese monkeys (Macaca fuscata fuscata). *Primates, 28*, 343-352.

Iversen, I. H., Ragnarsdottir, G., & Randrup, K. I. (1984). Operant conditioning of autogrooming in vervet monkeys (Cercopithecus aethiops). *Journal of the Experimental Analysis of Behavior, 42*, 171-189.

Jalles-Filho, E., Grassetto, R., de Cunha, T., & Salm, R. (2001). Transport of tools and mental representation: is capuchin monkey tool behaviour a useful model of plio-pleistocene hominid technology? *Journal of Human Evolution, 40*, 365-377.

Jarrold, C., Carruthers, P., Smith, P. K., & Boucher, J. (1994). Pretend play: Is it metarepresentational? *Mind and Language, 9*, 445-468.

Jolly, A. (1966). Lemur social behavior and primate intelligence. *Science, 153*, 501-506.

Kagan, J. (1981). *The second year.* Harvard University Press.

Karmiloff-Smith, A. (1986). From meta-processes to conscious access: Evidence from children's metalinguistic and repair data. *Cognition, 23*, 95-147.

Katz, J. S., Wright, A. A., & Bachevalier, J. (2002). Mechanisms of same/different abstract-concept learning by rhesus monkeys (Macaca mulatta). *Journal of Experimental Psychology: Animal Behavior Processes, 28,* 358-368.

Koehler, W. (1957). *The mentality of apes* (2^{nd} Ed.). Harmondsworth: Penguin Books.

Kuhlmeier, V. A., Boysen, S. T., & Mukobi, K. L. (1999). Scale-model comprehension by chimpanzees (Pan troglodytes). *Journal of Comparative Psychology, 113*, 396-402.

Ledbetter, D. H., & Basen, J. A. (1982). Failure to demonstrate self-recognition in gorillas. *American Journal of Primatology, 2*, 307-310.

Leslie, A. M. (1987). Pretense and representation: The origins of "theory of mind.". *Psychological Review, 94*, 412-426.

Lethmate, J., & Ducker, G. (1973). Experiments on self-recognition in a mirror in orangutans, chimpanzees, gibbons and several monkey species. *Zeitschrift Fur Tierpsychologie, 33*, 248-269.

Lewis, M., & Brooks-Gunn, J. (1979). *Social cognition and the acquisition of self.* New York: Plenum Press.

Lin, A. C., Bard, K. A., & Anderson, J. R. (1992). Development of self-recognition in chimpanzees (Pan troglodytes). *Journal of Comparative Psychology, 106,* 120-127.

Louboungou, M., & Anderson, J. R. (1987). Yawning, scratching, and protruded lips: Differential conditionability of natural acts in pigtail monkeys (Macaca nemestrina). *Primates, 28*, 367-375.

Maestripieri, D. (1996). Gestural communication and its cognitive implications in pigtail macaques (Macaca nemestrina). *Behaviour, 133*, 997-1022.

Marchal, P., & Anderson, J. R. (1993). Mirror-image responses in capuchin monkeys (Cebus capucinus): Social responses and use of reflected environmental information. *Folia Primatologica, 61*, 165-173.

Matsuzawa, T. (1985). Use of numbers by a chimpanzee. *Nature, 315*, 57-59.

Matsuzawa, T. (1991). Nesting cups and metatools in chimpanzees. *Behavioral and Brain Sciences, 14*, 570-571.

Meltzoff, A. N. (1990). Foundations for developing a concept of self: The role of imitation in relating self to other and the value of social mirroring, social modeling, and self practice in infancy. In: Cicchetti, D., & Beeghly, M. (eds), *The self in transition: Infancy to childhood.* (pp.139-164). Chicago: University of Chicago Press.

Meltzoff, A. N. (1995). Understanding the intentions of others: Re-enactment of intended acts by 18-month-old children. *Developmental Psychology, 31*, 838-850.

Meltzoff, A. N. (1996). The human infant as imitative generalist: A 20-year progress report on infant imitation with implications for comparative psychology. In: Heyes, C. M. & Galef, B. G., (eds), *Social learning in animals: The roots of culture.* (pp.347-370). San Diego: Academic Press.

Meltzoff, A. N., & Gopnik, A. (1989). On linking nonverbal imitation, representation, and language learning in the first two years of life. In: Speidel, G. E., & Nelson, K. E. (eds), *The many faces of imitation in language learning.* (pp. 23-51). Berlin:

Springer.

Meltzoff, A. N., & Gopnik, A. (1994). The role of imitation in understanding persons and developing a theory of mind. In: Baron-Cohen, S., Tager-Flusberg, H., & Cohen, D. J. (eds), *Understanding other minds: Perspectives from autism.* (pp.335-366). London: Oxford University Press.

Meltzoff, A. N., & Moore, M. (1977). Imitation of facial and manual gestures by human neonates. *Science, 198,* 75-78.

Mendes, N., & Huber, L. (2004). Object permanence in common marmosets (Callithrix jacchus). *Journal of Comparative Psychology, 118,* 103-112.

Mendl, M., & Paul, E. S. (2004). Consciousness, emotion and animal welfare: Insights from cognitive science. *Animal Welfare, 13,* S17-S25.

Menzel, C. R. (1999). Unprompted recall and reporting of hidden objects by a chimpanzee (Pan troglodytes) after extended delays. *Journal of Comparative Psychology, 113,* 426-434.

Menzel, E., Savage-Rumbaugh, E., & Lawson, J. (1985). Chimpanzee (Pan troglodytes) spatial problem solving with the use of mirrors and televised equivalents of mirrors. *Journal of Comparative Psychology, 99,* 211-217.

Mercado, E. I., Murray, S. O., Uyeyama, R. K., Pack, A. A., & Herman, L. M. (1998). Memory for recent actions in the bottlenosed dolphin (Tursiops truncatus): Repetition of arbitrary behaviors using an abstract rule. *Animal Learning and*

Behavior, 26, 210-218.

Mercado, E. I., Uyeyama, R. K., Pack, A. A., & Herman, L. M. (1999). Memory for action events in the bottlenosed dolphin. *Animal Cognition, 2,* 17-25.

Miles, H. W. (1994). Me Chantek: The development of self-awareness in a signing orangutan. In: Parker, S. T., Mitchell, R. W., & Boccia, M. L. (eds), *Self-awareness in animals and humans: Developmental perspectives.* (pp.254-272). New York: Cambridge University Press.

Miles, H. W., Mitchell, R. W., & Harper, S. E. (1996). Simon says: The development of imitation in an enculturated orangutan. In: Russon, A. E., Bard, K. A., & Parker, S. T. (eds), *Reaching into thought: The minds of the great apes.* (pp.278-299). New York: Cambridge University Press.

Mischel, W., & Mischel, H. (1977). Self control and the self. In: Mischel, T. (Ed), *The Self: Psychological and philosophical issues.* (pp.31-64). London: Blackwell.

Mischel, W., Shoda, Y., & Rodriguez, M. L. (1989). Delay of gratification in children. *Science, 244,* 933-938.

Mitchell, R. W. (1993). Mental models of mirror-self-recognition: Two theories. *New Ideas in Psychology, 11,* 295-325.

Mitchell, R. W. (2002). Kinesthetic-visual matching, imitation, and self-recognition. In: Bekoff, M., Allen, C., & Burghardt, G. (eds), *The cognitive animal.* (pp.345-351). Cambridge: MIT Press.

Mitchell, R. W., & Anderson, J. R. (1993). Discrimination learning of scratching, but failure to obtain imitation and self-recognition in a long-tailed macaque. *Primates, 34*, 301-309.

Moore, B. R. (1996). The evolution of imitative learning. In: Heyes, C. M. & Galef, B. G. (eds), *Social learning in animals: The roots of culture.* (pp.245-265). San Diego: Academic Press.

Moore, C., Jarrold, C., Russell, J., Lumb, A., Sapp, F., & MacCallum, F. (1995). Conflicting desire and the child's theory of mind. *Cognitive Development, 10*, 467-482.

Myowa-Yamakoshi, M., Tomonaga, M., Tanaka, M., & Matsuzawa, T. (2004). Imitation in neonatal chimpanzees (Pan troglodytes). *Developmental Science, 7*, 437-442.

Nadel, J. (2002). Imitation and imitation recognition: Functional use in preverbal infants and nonverbal children with autism. In: Meltzoff, A. N., & Prinz, W. (eds), *The imitative mind: Development, evolution, and brain bases.* (pp.42-62). New York: Cambridge University Press.

Natale, F., & Antinucci, F. (1989). Stage 6 object-concept and representation. In: Antinucci, F. (Ed), *Cognitive structure and development in nonhuman primates.* (pp.97-112). Hillsdale: Lawrence Erlbaum Associates.

Natale, F., Antinucci, F., Spinozzi, G., & Poti, P. (1986). Stage 6 object concept in nonhuman primate cognition: A comparison between gorilla (Gorilla gorilla gorilla) and Japanese macaque (Macaca fuscata). *Journal of Comparative Psychology, 100*, 335-339.

Nielsen, M., Collier-Baker, E., Davis, J. M., & Suddendorf, T. (2005). Imitation recognition in a captive chimpanzee (Pan troglodytes). *Animal Cognition, 8*, 31-36.

O'Reilly, A. W. (1995). Using representations: Comprehension and production of actions with imagined objects. *Child Development, 66*, 999-1010.

Panger, M., Perry, S., Rose, L., Gros-Louis, J., Vogel, E., Mackinnon, K., & Baker, M. (2002). Cross-site differences in foraging behavior of white-faced capuchins (Cebus capucinus). *American Journal of Physical Anthropology, 19*, 52-66.

Parker, S. T., & McKinney, M. L. (1999). *Origins of intelligence: The evolution of cognitive development in monkeys, apes, and humans.* Baltimore: Johns Hopkins University Press.

Patterson, F., & Cohen, R. (1994). Self-recognition and self-awareness in lowland gorillas. In: Parker, S. T., Mitchell, R. W., & Boccia, M. L. (eds), *Self-awareness in humans and animals.* (pp. 273-290). Cambridge: Cambridge University Press.

Perner, J. (1990). Experiential awareness and children's episodic memory. In: Schneider, W., & Weinert, F. E. (eds), *Interactions among aptitudes, strategies and knowledge in cognitive performance.* (pp. 3-11). New York: Springer.

Perner, J. (1991). *Understanding the representational mind.* Cambridge: MIT Press.

Perner, J. (2001). Episodic memory: Essential distinctions and developmental implications. In: Moore, C., & Lemmon, K. (eds), *The self in time: Developmental perspectives.*

(pp.181-202). Mahwah: Lawrence Erlbaum Associates.

Perner, J., & Ruffman, T. (1995). Episodic memory an autonoetic consciousness: Developmental evidence and a theory of childhood amnesia. *Journal of Experimental Child Psychology, 59*, 516-548.

Piaget, J. (1952). *The origins of intelligence in children.* Oxford: International Universities Press.

Piaget, J. (1954). *The construction of reality in the child.* Oxford: Basic Books.

Pierce, J. D. (1985). A review of attempts to condition operantly alloprimate vocalizations. *Primates, 26*, 202-213.

Platt, M. M., & Thompson, R. L. (1985). Mirror responses in a Japanese macaque troop. *Primates, 26*, 300-314.

Poss, S. R., & Rochat, P. (2003). Referential understanding of videos in chimpanzees (Pan troglodytes), orangutans (Pongo pygmaeus), and children (Homo sapiens). *Journal of Comparative Psychology, 117*, 420-428.

Poti, P., & Spinozzi, G. (1994). Early sensorimotor development in chimpanzees (Pan troglodytes). *Journal of Comparative Psychology, 108*, 93-103.

Povinelli, D. J. (1994). How to create self-recognizing gorillas (but don't try it on macaques). In: Parker, S. T., Mitchell, R. W., & Boccia, M. L. (eds), *Self-awareness in animals and humans: Developmental perspectives.* (pp.291-300). New York: Cambridge University Press.

Povinelli, D. J., Gallup, G. G. Jr., Eddy, T. J., & Bierschwale, D. T. (1997). Chimpanzees recognize themselves in mirrors. *Animal Behaviour, 53*, 1083-1088.

Povinelli, D. J., Landau, K. R., & Perilloux, H. K. (1996). Self-recognition in young children using delayed versus live feedback: Evidence of a developmental asynchrony. *Child Development, 67,* 1540-1554.

Povinelli, D. J., Rulf, A. B., Landau, K. R., & Bierschwale, D. T. (1993). Self-recognition in chimpanzees (Pan troglodytes): Distribution, ontogeny, and patterns of emergence. *Journal of Comparative Psychology, 107*, 347-372.

Premack, D., & Woodruff, G. (1978). Does the chimpanzee have a theory of mind? *Behavioral and Brain Sciences, 1*, 515-526.

Pylyshyn, Z. W. (1978). Computational models and empirical constraints. *Behavioral and Brain Sciences, 1*, 93-127.

Riviello, M. C., Visalberghi, E., & Blasetti, A. (1993). Individual differences in responses toward a mirror by captive tufted capuchin monkeys (Cebus apella). *Hystrix, 4*, 35-44.

Rizzolatti, G., Fadiga. L, Gallese, V., & Fogassi, L. (1996). Premotor cortex and the recognition of motor actions. *Cognitive Brain Research, 3*, 131-141.

Rowe, N. (1996). *The pictorial guide to the living primates*. Charlestown: Pogonias Press.

Rumbaugh, D., & Pate, J. (1984). Primates' learning by levels. In: Greenberg, G., & Tobach, E. (eds), *Behavioral evolution and integrative levels.* (pp.221-240).

Hillsdale: Lawrence Erlbaum.

Russon, A. E. (1996). Imitation in everyday use: Matching and rehearsal in the spontaneous imitation of rehabilitant orangutans (Pongo pygmaeus). In: Russon, A. E., Bard, K. A., & Parker, S. T. (eds), *Reaching into thought: The minds of the great apes.* (pp.152-176). New York: Cambridge University Press.

Schacter, D. L. (1987). Implicit memory: History and current status. *Journal of Experimental Psychology: Learning Memory and Cognition, 13*, 501-518.

Schulman, A. H., & Kaplowitz, C. (1977). Mirror-image response during the first two years of life. *Developmental Psychobiology, 10*, 133-142.

Schwartz, B. L., Colon, M., Sanchez, I., Rodriguez, I., & Evans, S. (2002). Single-trial learning of "what" and "who" information in a gorilla (Gorilla gorilla gorilla): implications for episodic memory. *Animal Cognition, 5*, 85-90.

Schwartz, B. L., & Evans, S. (2001). Episodic memory in primates. *American Journal of Primatology, 55*, 71-85.

Shillito, D. J., Gallup, G. G. Jr., & Beck, B. B. (1999). Factors affecting mirror behaviour in western lowland gorillas, Gorilla gorilla. *Animal Behaviour, 57*, 999-1004.

Siegel, S., & Castellan, N. Jr. (1988). *Nonparametric statistics for the behavioral sciences (2nd Ed.).* New York: Mcgraw-Hill Book Company.

Smith, L. B., & Thelen, E. (2003). Development as a dynamic system. *Trends in Cognitive Sciences, 7*, 343-348.

Suarez, S. D., & Gallup, G. G. Jr. (1981). Self-recognition in chimpanzees and orangutans, but not gorillas. *Journal of Human Evolution, 10*, 175-188.

Suarez, S. D., & Gallup, G. G. Jr. (1986). Face touching in primates: A closer look. *Neuropsychologia, 24*, 597-600.

Suarez, S. D., & Gallup, G. G. Jr. (1986). Social responding to mirrors in rhesus macaques (Macaca mulatta): Effects of changing mirror location. *American Journal of Primatology, 11*, 239-244.

Suddendorf, T. (1999). The rise of the metamind. In: Corballis, M. C., & Lea, S. E. G. (eds), *The descent of mind: Psychological perspectives on hominid evolution.* (pp.218-260). London: Oxford University Press.

Suddendorf, T., & Corballis, M. C. (1997). Mental time travel and the evolution of the human mind. *Genetic, Social, and General Psychology Monographs, 123*, 133-167.

Suddendorf, T., & Whiten, A. (2001). Mental evolution and development: Evidence for secondary representation in children, great apes, and other animals. *Psychological Bulletin, 127,* 629-650.

Sugiyama, Y. (1995). Tool-use for catching ants by chimpanzees at Bossou and Monts Nimba, West Africa. *Primates, 36*, 193-205.

Swartz, K. B., & Evans, S. (1991). Not all chimpanzees (Pan troglodytes) show self-recognition. *Primates, 32*, 483-496.

Tayler, C., & Saayman, G. (1973). Imitative behaviour by Indian Ocean bottlenose dolphins (Tursiops aduncus) in captivity. *Behaviour, 44,* 286-298.

Thompson, R. L., & Boatright Horowitz, S. L. (1994). The question of mirror-mediated self-recognition in apes and monkeys: Some new results and reservations. In: Parker, S. T., Mitchell, R. W., & Boccia, M. L. (eds), *Self-awareness in animals and humans: Developmental perspectives.* (pp.330-349). New York: Cambridge University Press.

Tomasello, M., & Barton, M. E. (1994). Learning words in nonostensive contexts. *Developmental Psychology, 30*, 639-650.

Tomasello, M., & Call, J. (1997). *Primate cognition.* London: Oxford University Press.

Tomasello, M., Kruger, A., & Ratner, H. (1993). Cultural learning. *Behavioral and Brain Sciences, 16,* 495-552.

Tomonaga, M., Tanaka, M., Matsuzawa, T., Myowa-Yamakoshi, M., Kosugi, D., Mizuno, Y., Okamoto, S. (2004). Development of social cognition in infant chimpanzees (Pan troglodytes): Face recognition, smiling, gaze, and the lack of triadic interactions. *Japanese Psychological Research, 46,* 227-235.

Tulving, E. (1972). Episodic and semantic memory. In: Tulving, E., & Donaldson, W. (eds), *Organization of memory.* (pp. 381-403). Oxford: Academic Press.

Tulving, E. (1985). How many memory systems are there? *American Psychologist, 40,* 385-398.

Tulving, E. (1998). Brain/mind correlates of human memory. In: Sabourin, M., Craik, F., &

Robert, M. (eds), *Advances in psychological science, Vol. 2: Biological and cognitive aspects.* (pp.441-460). Hove: Psychology Press/Erlbaum (UK) Taylor & Francis.

Tulving, E. (2005). Episodic memory and autonoesis: uniquely human? In: Terrace, H. & Metcalfe, J. (eds), *The missing link in cognition.* (pp.3-56). Oxford: Oxford University Press.

Tulving, E., & Markowitsch, H. J. (1998). Episodic and declarative memory: Role of the hippocampus. *Hippocampus, 8*, 198-204.

Ujhelyi, M., Merker, B., Buk, P., & Geissmann, T. (2000). Observations on the behavior of gibbons (Hylobates leucogenys, H. gabriellae, and H. lar) in the presence of mirrors. *Journal of Comparative Psychology, 114,* 253-262.

Verbeek, P., & de Waal, F. B. M. (1997). Postconflict behavior in captive brown capuchins in the presence and absence of atrractive food. *Internatinal Journal of Primatology, 18*, 703-725.

Visalberghi, E. (1990). Tool use in Cebus. *Folia Primatologica, 54,* 146-154.

Visalberghi, E. (1997). Success and understanding in cognitive tasks: A comparison between Cebus apella and Pan troglodytes. *International Journal of Primatology, 18*, 811-830.

Visalberghi, E. (2000). Tool use behavior and the understanding of causality in primates. In: Thommen, E., & Kilcher, H. (eds), *Comparer ou predire: exemples de* *recherches comparatives en psychologie aujourd'hui.* (pp. 17-35). Editions Universitaires Fribourg.

Visalberghi, E., & Fragaszy, D. M. (1990). Do monkeys ape? In: Parker, S. T., & Gibson, K. R. (eds), *"Language" and intelligence in monkeys and apes: Comparative developmental perspectives.* (pp.247-273). New York: Cambridge University Press.

Visalberghi, E., & Fragaszy, D. M. (2002). "Do monkeys ape?": Ten years after. In: Dautenhahn, K., & Nehaniv, C. L. (eds), *Imitation in animals and artifacts.* (pp.471-499). Cambridge: MIT Press.

Visalberghi, E., Fragaszy, D. M., & Savage Rumbaugh, S. (1995). Performance in a tool-using task by common chimpanzees (Pan troglodytes), bonobos (Pan paniscus), an orangutan (Pongo pygmaeus), and capuchin monkeys (Cebus apella). *Journal of Comparative Psychology, 109*, 52-60.

Visalberghi, E., & Limongelli, L. (1994). Lack of comprehension of cause-effect relations in tool-using capuchin monkeys (Cebus apella). *Journal of Comparative Psychology, 108*, 15-22.

Visalberghi, E., & Limongelli, L. (1996). Acting and understanding: Tool use revisited through the minds of capuchin monkeys. In: Russon, A. E., Bard, K. A., & Parker, S. T. (eds), *Reaching into thought: The minds of the great apes.* (pp.57-79). New York: Cambridge University Press.

Visalberghi, E., & Tomasello, M. (1998). Primate causal understanding in the physical and psychological domains. *Behavioural Processes, 42*, 189-203.

Visalberghi, E., & Trinca, L. (1989). Tool use in capuchin monkeys: Distinguishing between performing and understanding. *Primates, 30*, 511-521.

Voelkl, B., & Huber, L. (2000). True imitation in marmosets. *Animal Behaviour, 60*, 195-202.

von Eckardt, B. (1999). Mental representation. In: Wilson, R., & Keil, F. (eds), *The MIT Encyclopedia of the Cognitive Sciences.* (pp.527-529). Cambridge: MIT Press.

Walraven, V., van Elsacker, L., & Verheyen, R. (1995). Reactions of a group of pygmy chimpanzees (Pan paniscus) to their mirror-images: Evidence of self-recognition. *Primates, 36*, 145-150.

Washburn, D. A., & Astur, R. S. (1998). Nonverbal working memory of humans and monkeys: Rehearsal in the sketchpad? *Memory and Cognition, 26*, 277-286.

Weigel, R. M. (1978). The facial expressions of the brown capuchin monkey (Cebus apella). *Behaviour, 68*, 250-276.

Wheeler, M. A., Stuss, D. T., & Tulving, E. (1997). Toward a theory of episodic memory: The frontal lobes and autonoetic consciousness. *Psychological Bulletin, 121*, 331-354.

Whiten, A. (1996). Imitation, pretense, and mindreading: Secondary representation in comparative primatology and developmental psychology? In: russon, A. E., Bard, K. A., & Parker, S. T. (eds), *Reaching into thought: The minds of the great apes.* (pp.300-324). New York: Cambridge University Press.

Whiten, A., & Ham, R. (1992). On the nature and evolution of imitation in the animal kingdom. In: Slater, P., Rosenblatt, C., & Milinski, M. (eds), *Advances in the Study of Behavior.* (pp.239-283). New York: Academic Press.

Wimmer, H., Hogrefe, G. J., & Perner, J. (1988). Children's understanding of informational access as source of knowledge. *Child Development, 59*, 386-396.

Wimmer, H., & Perner, J. (1983). Beliefs about beliefs: Representation and constraining function of wrong beliefs in young children's understanding of deception. *Cognition, 13*, 103-128.

Wrangham, R. W., & Peterson, D. (1996). *Demonic males: Apes and the origins of human violence.* Boston: Houghton Mifflin Co.

Yunger, J. L., & Bjorklund, D. F. (2004). An assessment of generalization of imitation in two enculturated orangutans (Pongo pygmaeus) . *Journal of Comparative Psychology, 118,* 242-246.

Zahn-Waxler, C., Radke-Yarrow, M., & King, R. A. (1979). Child rearing and children's prosocial initiations toward victims of distress. *Child Development, 50*, 319-330.

Zentall, T. R. (1996). An analysis of imitative learning in animals. In: Heyes, C. M., & Galef, B. G. (eds), *Social learning in animals: The roots of culture.* (pp.221-243). San Diego: Academic Press.

Appendix

Appendix to Chapter 2: Training data of two additional monkeys

As mentioned in Chapter 2, two additional monkeys (Papa and David) were trained to perform three self-directed behaviours (scratching, grooming, mouthing). However, they never learned to respond correctly to the repeat signal. This appendix documents their performance during training. For further details on subjects, housing and training, see Chapter 2.

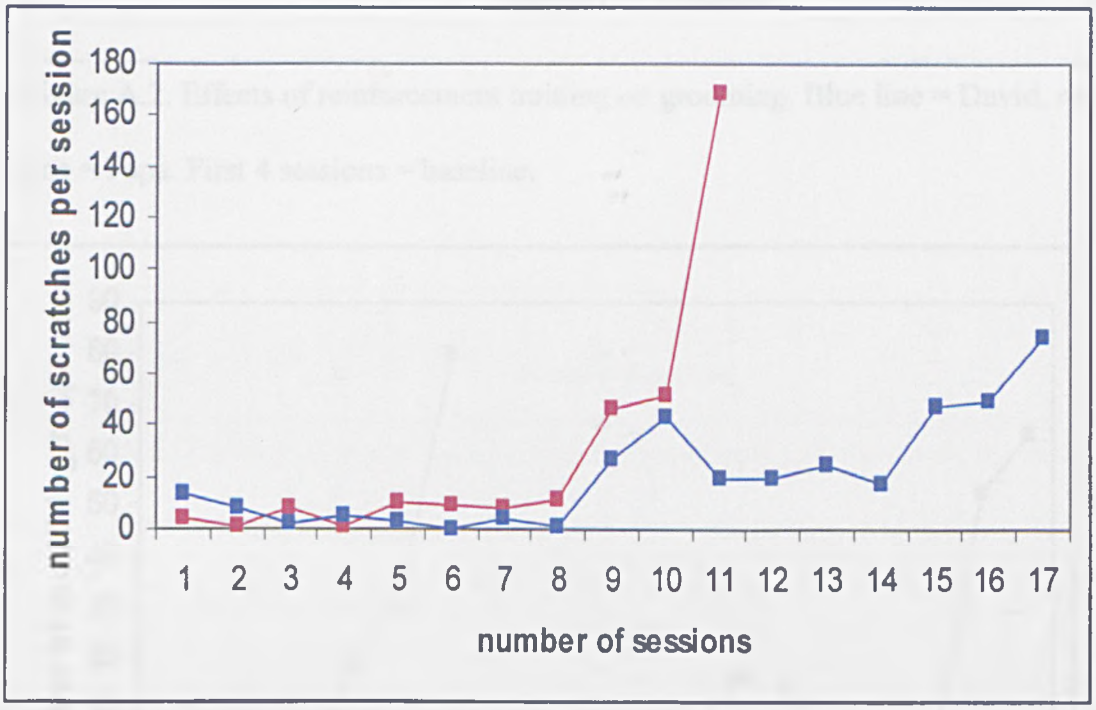

Figure A.1. Effects of reinforcement training on scratching. Blue line = David, red line = Papa. First 8 sessions = baseline.

Figure A.1. shows both monkeys' performances during continuous reinforcement of scratching responses. As can be seen, scratching increased dramatically following continuous reinforcement. Similar effects can be observed for grooming (Figure A.2.) and mouthing (Figure A.3.).

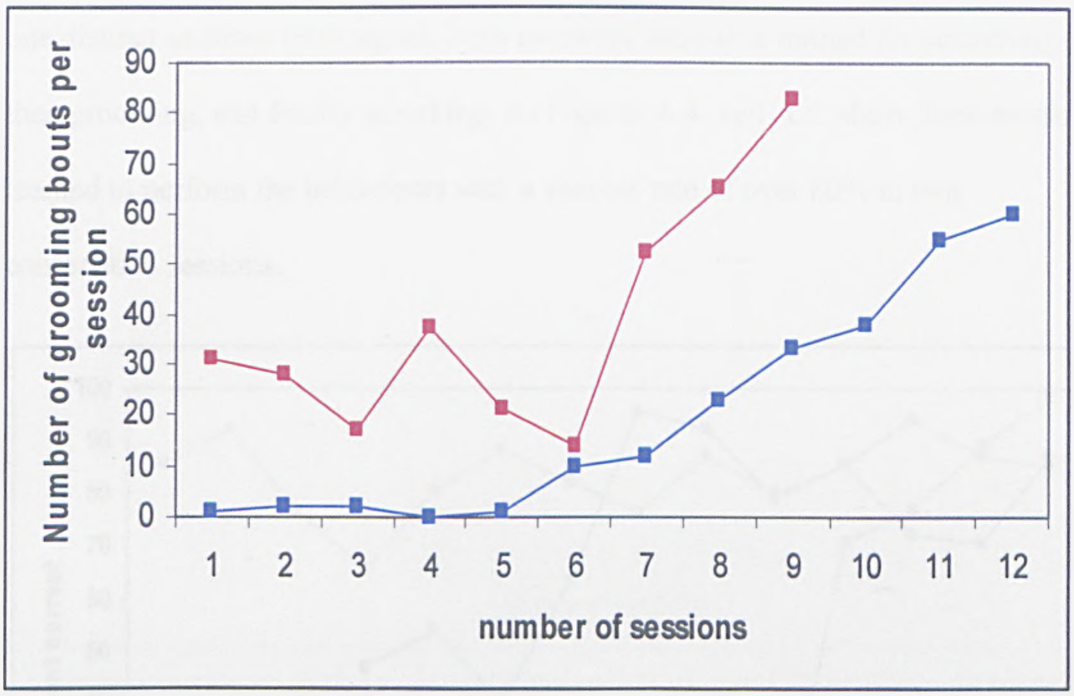

Figure A.2. Effects of reinforcement training on grooming. Blue line = David, red line = Papa. First 4 sessions = baseline.

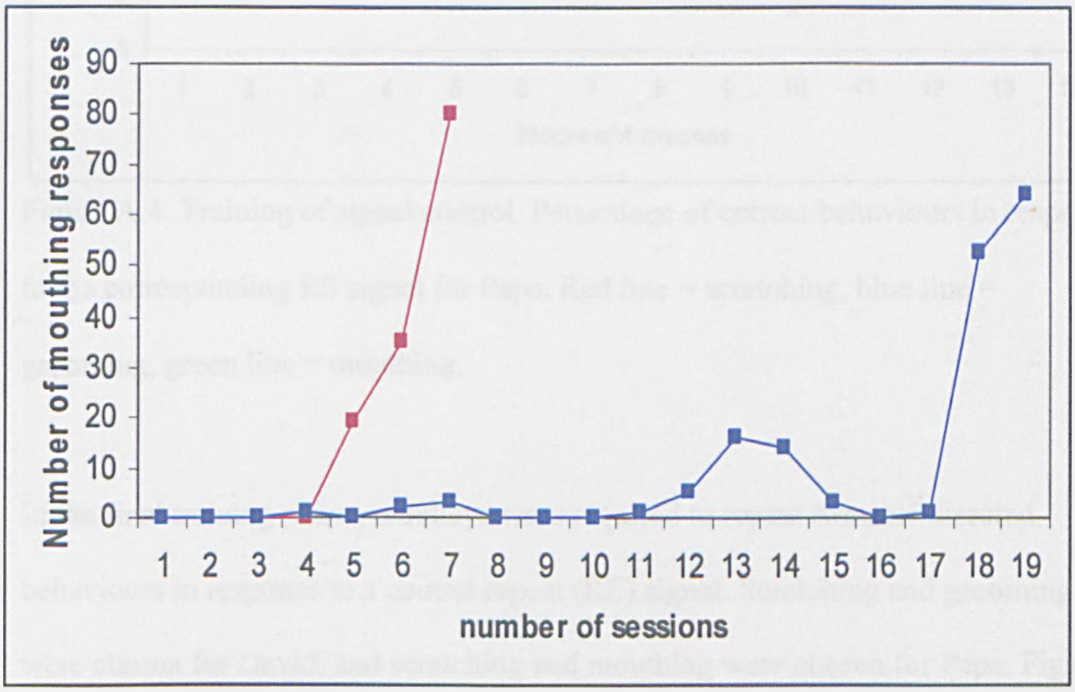

Figure A.3. Effects of reinforcement training on mouthing. Blue line = David, red line = Papa. First 4 sessions = baseline

The second training step was to train the monkeys to associate each behaviour with one distinct auditory (BS) signal. Both monkeys were first trained for scratching, then grooming, and finally mouthing. As Figures A.4. and A.5. show, both monkeys learned to perform the behaviours with a success rate of over 80% in two consecutive sessions.

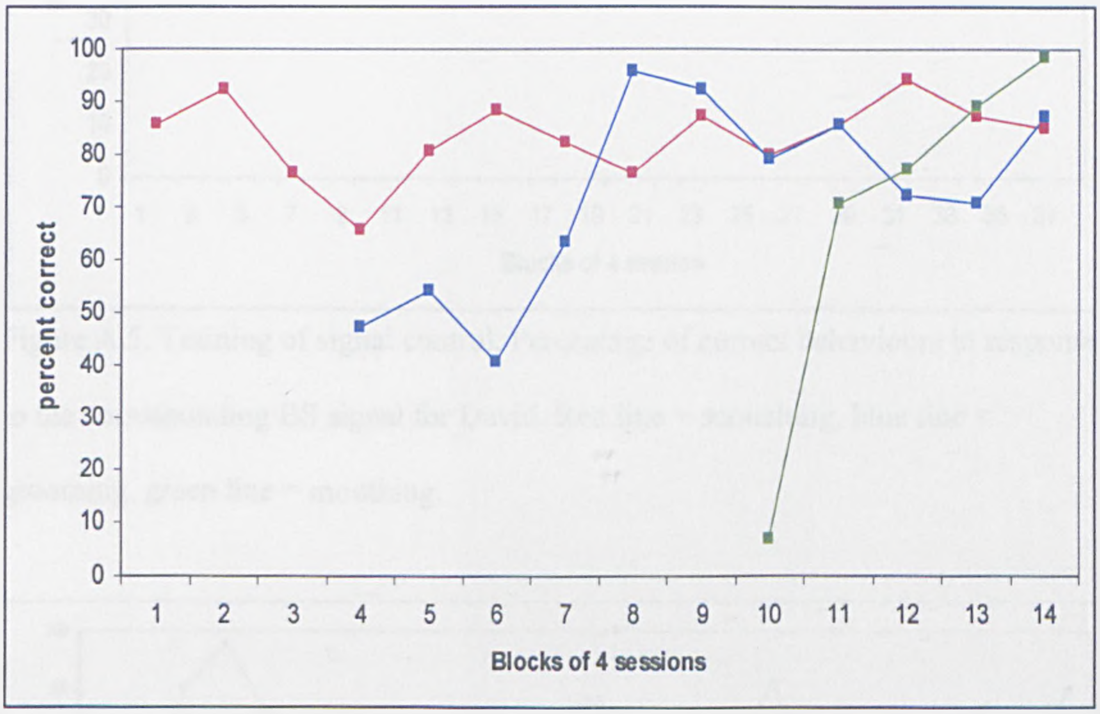

Figure A.4. Training of signal control. Percentage of correct behaviours in response to the corresponding BS signal for Papa. Red line = scratching, blue line = grooming, green line = mouthing.

In the final training phase, monkeys were required to repeat two self-directed behaviours in response to a neutral repeat (RE) signal. Scratching and grooming were chosen for David, and scratching and mouthing were chosen for Papa. Figures A.6 and A.7. show that despite intensive training, neither monkey learned to repeat the target behaviours at 80% correct or more over two sessions. Due to time pressures, both monkeys were therefore dropped from the experiment.

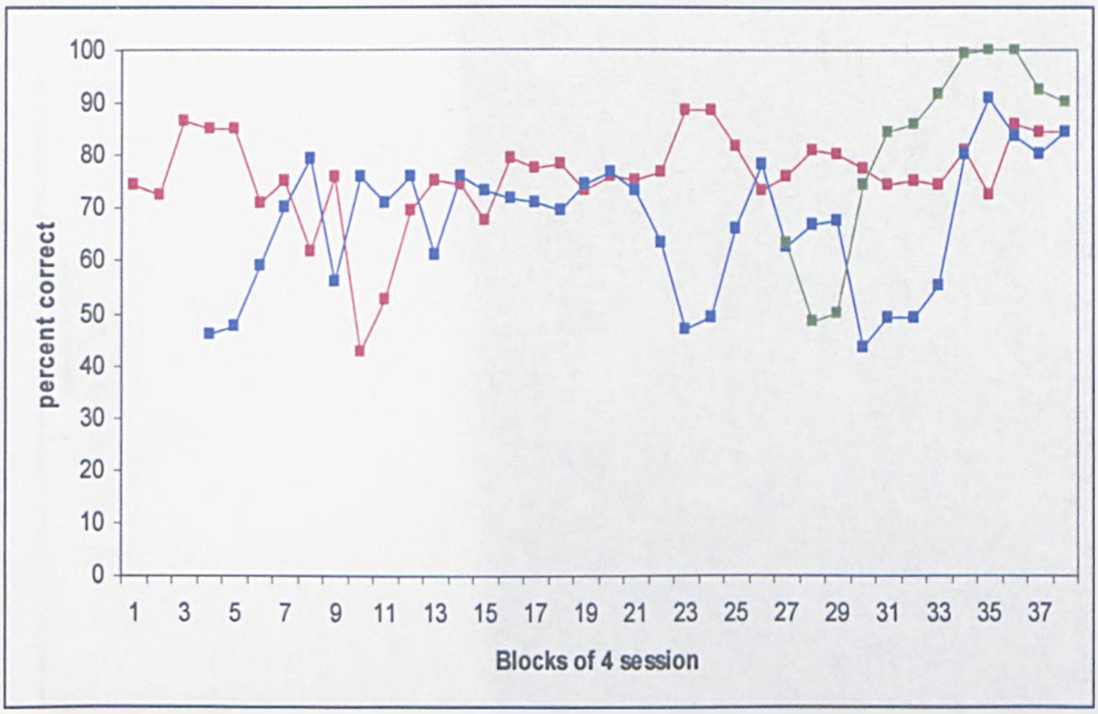

Figure A.5. Training of signal control. Percentage of correct behaviours in response to the corresponding BS signal for David. Red line = scratching, blue line = grooming, green line = mouthing.

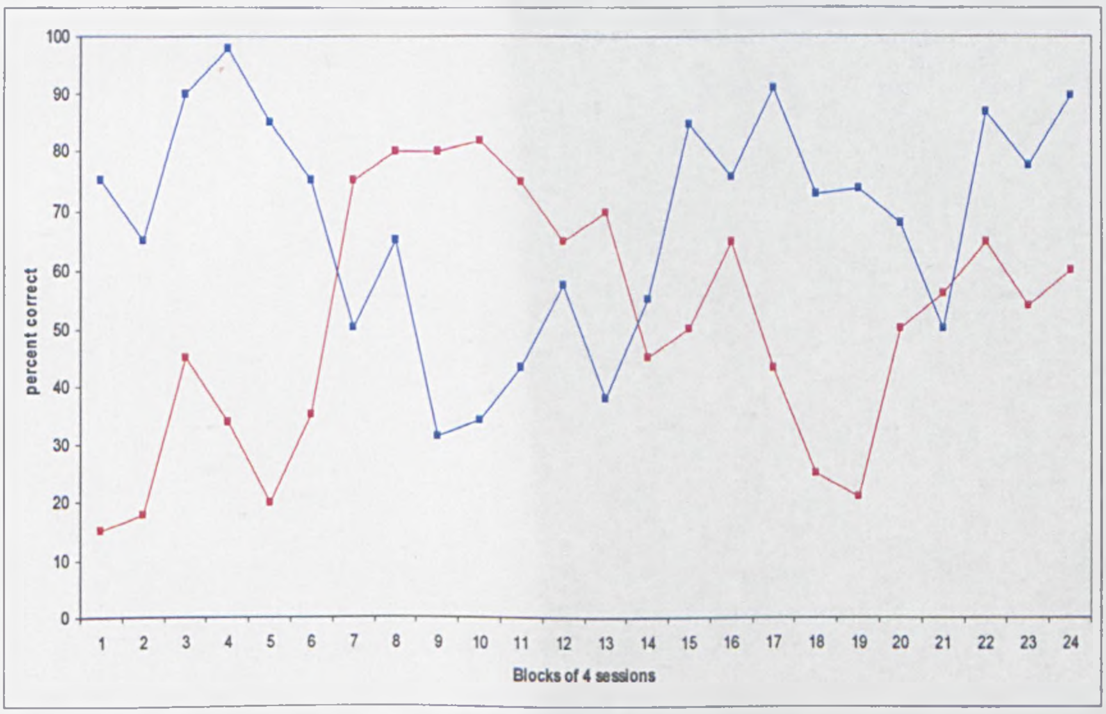

Figure A.6. Training to the RE signal. Percentage of correct repetitions in response to the RE signal for Papa. Red line = scratching, blue line = grooming.

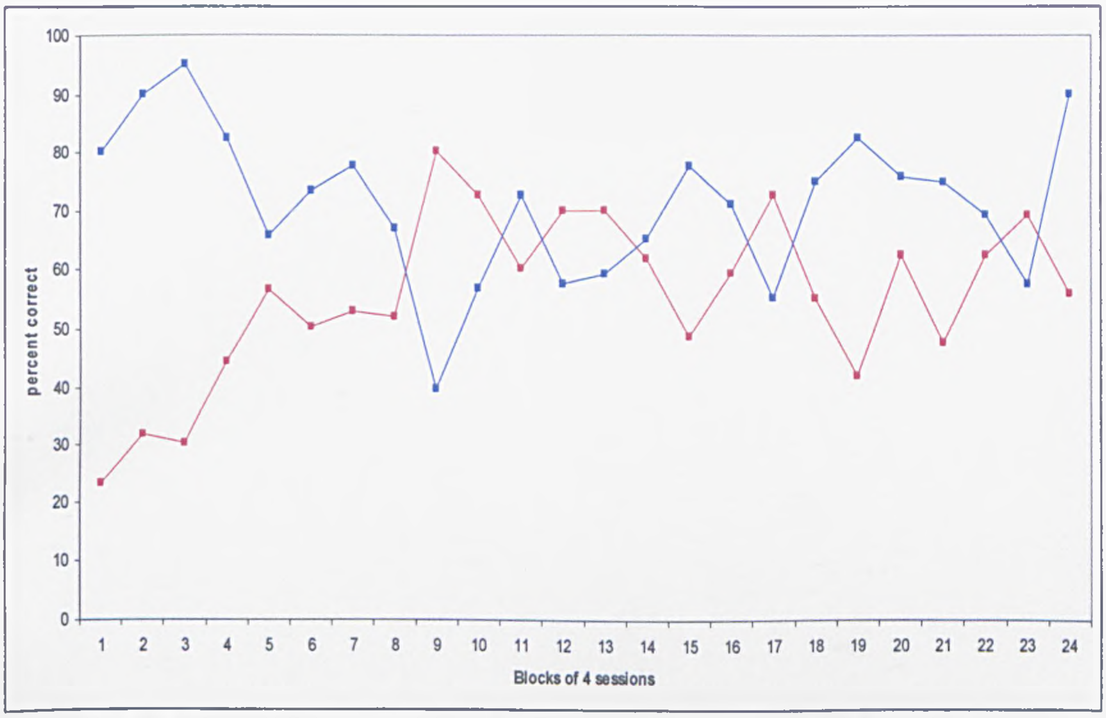

Figure A.7. Training to the RE signal. Percentage of correct repetitions in response to the RE signal for David. Red line = scratching, blue line = grooming.