A COMPARATIVE APPROACH TO SOCIAL LEARNING
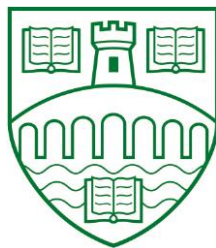
FROM THE BOTTOM UP

Eóin P. O' Sullivan

Thesis submitted for the degree of Doctor of Philosophy

Psychology Division

University of Stirling

September 2015

Abstract

The aim of this thesis is to examine the cognitive processes of social learning from the bottom up. In the field of comparative psychology, an overemphasis on understanding complex cognitive processes in nonhuman animals (e.g. empathy, imitation), may be detrimental to the study of simpler mechanisms. In this thesis, I report five studies of simple cognitive processes related to social learning. A series of experiments with human children and capuchin monkeys (*Sapajus sp.*), examined action imitation and identified a possible role for associative learning in the development of this ability. An analysis of observational data from captive capuchins explored a number of lesser-studied social learning phenomena, including behavioural synchrony, the neighbour effect, and group-size effects. The results of this study emphasise the importance of exploring behaviour at a number of levels to appreciate the dynamic nature of social influence. Two final experiments examined social contagion in capuchin monkeys, and highlight the importance of describing the relationship between behaviour and emotion to properly understand more complex social cognition. Together, these studies demonstrate how approaching human and nonhuman behaviour from the bottom up, as well as from the top down, can contribute to a better comparative science of social learning.

Acknowledgements

and piloting the study reported in Chapter 3.

At Stirling, thanks to the members of the Behaviour and Evolution Research Group, especially Prof Hannah Buchanan-Smith, Prof Phyllis Lee, Prof Jim Anderson and Dr Sarah-Jane Vick, for your constant encouragement, and your passion for animal behaviour and cognition. I consider myself lucky to be a member of such a wonderful group. Also, a massive thank you to Aileen Schmidt and Sarah Thorburn for their help when working with the playgroup.

I am especially grateful to my supervisor, Prof Christine Caldwell, for years of encouragement, guidance, and enthusiasm for this work. Thank you for inspiring me to ask interesting questions, and to think carefully about the answers.

I would like to thank my friends, Claire McCarthy, Shane Walsh, Phil Stack, Melissa Knox, Callum Knox, Malavika Narayana, Michelle Klailova, and Adam Milligan for their years of friendship, encouragement, and advice. Thanks to Olivia Kirtley and Caroline Allen – "PhD-ers in crime". It's been a bumpy ride-but it's been easier with friends.

I thank my partner, Cara Mannix, for her patience when I ramble, her ear when I rant, and her friendship, always. And finally, I thank my family. I cannot describe the gratitude I feel towards my parents and to my brothers and sister who continue to do so much for me. Thank you all.

Sin é.

Contents

Chapter 1: General Introduction

Social learning occurs when the behaviour of an animal is influenced by the behaviour, the results of behaviour, or the presence of another animal (adapted from Heyes, 1994). Evidence of social learning has been reported in a panoply of taxa. Wild populations of chimpanzees display socially learned behavioural traditions (Whiten et al., 1999), while sticklebacks learn about foraging locations from conspecifics (van Bergen, Coolen, & Laland, 2004). Female fruit flies use social cues to decide on the best substrate for egg-laying (Sarin & Dukas, 2009), and humans are so reliant on learning from other humans that some believe our superior social learning skills could be a key factor in the evolution of our large brains (Whiten & van Schaik, 2007).

While it is unsurprising that social animals use social information in adaptive ways, the diversity of social learning throughout the animal kingdom leaves us questioning whether all social learning is equal. Common-sense (as well as empirical studies) tells us that human cognition is vastly different from that of a fly, encouraging us to categorise a spectrum of processes that range from cognitively simple to complex. Social learning in invertebrates will be of a simple kind, reliant on processes of associative learning known to be taxonomically widespread in both vertebrates (Macphail, 1982) and

invertebrates (McConnell, 1966), while primate social learning will often require more complex cognitive processes (Whiten, Horner, Litchfield, & Marshall-Pescini, 2004). In the field of comparative psychology, the human mind is often considered a yardstick against which to compare the minds of our closest evolutionary relatives, particularly other primates (for a discussion see Barrett, Henzi, & Rendall, 2007; Heyes, 2012a). This a priori assumption regarding the complexity of processes that determine human behaviour ignores the many cognitive parallels humans and other animals share. Simple processes are likely to regulate many socially influenced behaviours in humans and in other primates, but often this line of research is ignored. In the course of this thesis I will consider the importance of so-called "simple" mechanisms of social learning and examine their role in primate behaviour. By highlighting the importance of these simple mechanisms and the role of associative processes in social learning, we can enrich our understanding of how animals, both human and nonhuman, learn from each other.

Differentiating the mechanisms of social learning

The definition of social learning provided in the opening line is not controversial, appearing often in texts covering the topic (e.g. Hoppitt & Laland, 2013; van de Waal, Claidière, & Whiten, 2013). However, when it comes to specific mechanisms of social learning, historically there has been little

consensus over the meaning of exact terms. For example, Byrne and Russon (1998) describe a hierarchical approach to imitation. Under their paradigm imitation occurs at the level of unique actions but also at the level of action-sequences. Alternatively, Voelkl and Huber (2000) describe "true imitation" occuring when an animal is biased toward the use of a particular action (i.e. the use of a particular bodypart to perform an action) after observing the same action performed by a demonstrator. In the following section I will define many of the commonly studied mechanisms of social learning, but this list will not be exhaustive (for a summary of the history of social learning mechanisms see Hoppitt & Laland, 2013). Instead, this introduction to the terminology of social learning research will act as a basis on which to highlight some important limitations of a comparative psychology of social learning.

The scope of social learning research is vast. A wide range of social learning mechanisms have been described over the last few decades (Galef, 1988; Heyes, 1994; Hoppitt & Laland, 2008a; Whiten & Ham, 1992), and researchers are beginning to understand the complexity inherent in teasing these mechanisms apart, both theoretically and operationally. In previous literature, a distinction has sometimes been made between mechanisms of social learning and social influence (Whiten & Ham, 1992; Whiten, 2000). Social learning is thought to take place when an observer learns something new about their environment

through the observation of a conspecific (Whiten, 2000). For example, while standing in my living room I might *learn* that it is cold outside by observing people through my window wearing winter coats. Examples of social influence on the other hand occur when an animal's behaviour is altered by observing another individual, but nothing new about the environment is learned (Whiten, 2000); e.g. observing a friend pass by my window might *influence* me to leave my house to talk to them, but I may not *learn* anything new about my environment by doing so. Importantly, although nothing is learned directly through mechanisms of social influence, indirect learning can take place (Heyes, 1994; Hoppitt & Laland, 2013). For example, after leaving my house to talk to a friend (*social influence*) I may *learn* that it is cold outside. Examples of social learning and social influence are often examined together as "social leaning mechanisms" (Heyes, 1994; Hoppitt & Laland, 2008a, 2013) and will be treated as such here. However, three further distinctions are made. Social learning can take place when an individual is influenced by:

a) The behaviour of another,

b) The results or products of another's behaviour, and

c) The presence of another individual or group of individuals.

In other reviews similar distinctions have been made between learning from a behaviour itself and the products of behaviour (Call & Carpenter, 2002; Heyes, 1993). Here, a further distinction is made for the effect of presence.

Learning from behaviour

When learning from behaviour, the motor action of an individual influences the performance of the same motor action from an observer. A monkey might learn how to use her hand to pry off the lid of a canister (Voelkl & Huber, 2000), or a pigeon might learn to step on a treadle for a food reward rather than pecking (Zentall, Sutton, & Sherburne, 1996). An animal might be prompted to perform a yawn or a scratch, solely by observing another exhibit the same motor action (Feneran et al., 2013; Paukner & Anderson, 2006). In these cases, an animal changes its behaviour because of the action it observes, not because of the effect that action had on some element of the environment. In the following brief summary of how animals learn from behaviour, two mechanisms will be covered: Imitation and contagion.

Imitation

While imitation is the most studied mechanism of social learning, its definition is not universally agreed (for example Galef, 2013; Zentall, 2012). At its most

complex, imitation is defined as the ability of an animal to learn how to perform an action previously not present in its behavioural repertoire after seeing the action being performed by another individual (Byrne, 2002b). The intrinsic difficulty in determining whether any observed behaviour is truly novel has been widely discussed (Caldwell & Whiten, 2002; Zentall, 2012), and some have argued that a novel sequence of actions may better describe imitative learning (Byrne & Russon, 1998; Whiten, 1998). In contrast, others have suggested that action matching without understanding the intentions or goals of the individual being imitated is not "true imitation" (Tomasello & Call, 1997; Tomasello, Carpenter, Call, Behne, & Moll, 2005). For others, matching the topographical features of an action is sufficient (Heyes, 1994; van de Waal & Whiten, 2012; Voelkl & Huber, 2000). While it could be argued that the study of imitation has been muddied by such conceptual discrepancies, vigorous debate over the classification of imitation has encouraged researchers to seriously consider the cognitive mechanisms that may underlie the copying of an action. Due to the difficulties in evaluating the novelty of an action or identifying whether an imitator understands the intentions of the individual being imitated, the use of imitation here refers to the matching of topographical features of an action (e.g. van de Waal & Whiten, 2012; Voelkl & Huber, 2007).

Action imitation is thought to be particularly demanding in cognitive terms due to the "correspondence problem". The correspondence problem was described by Nehaniv and Dautenhahn (2002) as the difficulty faced by an observer in recreating an action that perceptually, cognitively, or motivationally corresponds to the actions of the model. If a dog is to imitate a human for example, how can she recreate an action performed by a human's hand when her own hand (or paw) is nether functionally or perceptually similar? This correspondence problem is also present when imitation occurs within a species. When a human observes the actions of another, the perceptual input gleaned from this observation rarely maps directly to the perceptual experience of the action performed by the self. For example, when learning a musical instrument the learner often sits facing the teacher, both holding an instrument. If the teacher asked the student to make a chord-shape solely by observing the teacher's actions it would be impossible to transpose the shape purely through the matching of visual input. Both visual representations are presented in Figure 1.1 from the perspective of the student (A – looking at a teacher's hand, B – looking at one's own hand). Considering the gestalt it is clear that the visual representations are different, but it is useful to draw attention to specific features. When observing the finger positions of the teacher (Figure 1.1-A) the entire chord-shape is situated at the bottom of the visual field with respect to the guitar neck; open strings on the guitar neck are nearer the top of the visual field. When observing one's own performance of the same shape (Figure 1.1-B)

7

the fingers are closer to the top of the visual field with open strings at the bottom. When considering individual finger placement, the teacher's ring-finger is positioned closest to the left-most edge of the visual field (see Figure 1.1.A-I), but the student's ring-finger is observed closer to the right-side of the visual field (see Figure 1.1.B–II). This example is extreme, but this correspondence problem is common when the topographical features of an action are to be matched. While it is unclear how this correspondence effect is overcome, some have suggested that the mirror neuron system, first identified in macaques in the 90s (see Chapter 2; di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996) might solve this problem and help bridge the correspondence gap. However, the cognitive processes required to convert an observed action into a corresponding motor response continue to puzzle psychologists.

Imitation has been studied in a number of species with varying results. One method of identifying imitation is through a two-action task. These studies incorporate an apparatus that can be operated in two different ways (e.g. a door that can be opened by pushing or pulling). One method is demonstrated to an observer by a model (e.g. the door is pushed open), and if observers tend to perform the same actions that they saw demonstrated, imitation is said to have occurred.

Figure 1.1. A representation of the visual perception of the motor action necessary to create the D-major chord on a guitar from the perspective of a student observing A) a teacher facing the student, and B) the student's own fingers on the neck of a guitar.

A)
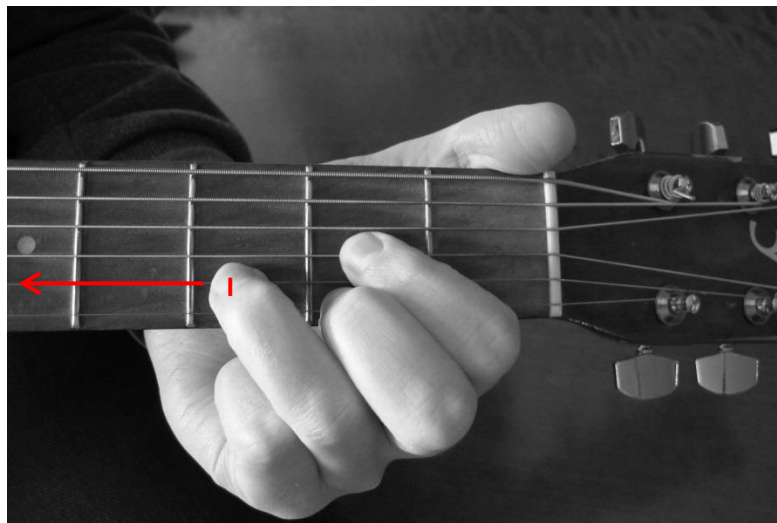
B)
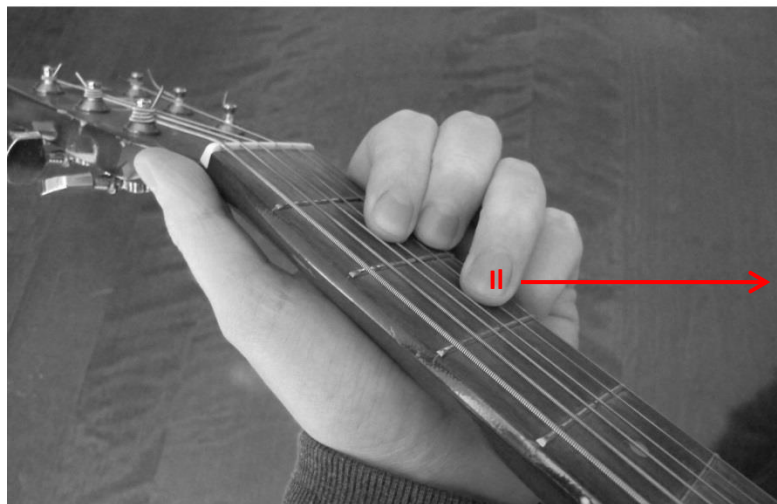
While the two-action method has been hugely successful in identifying evidence of social learning in animals (Dawson & Foss, 1965; Dindo, Whiten, & de Waal, 2009; Heyes & Dawson, 1990; Price & Caldwell, 2007; van de Waal et

al., 2013), it has been argued that many of these tasks do not sufficiently demonstrate action imitation as other social learning processes may account for the copying of actions (Heyes & Ray, 2000). For example, in some cases social learning may occur through object-movement re-enactment or emulation learning, both of which will be discussed later in greater detail.

More recently, researchers have adapted the two-action paradigm to account for this criticism. Instead of presenting subjects with an apparatus that can be operated in two different ways, researchers train model animals to interact with an apparatus using two different body parts (van de Waal & Whiten, 2012; Voelkl & Huber, 2000, 2007). If an apparatus can be opened using either hand actions or mouth action, then an individual who copies the action observed can be said to have imitated. Studies using this method have identified action imitation in Apes, New World, and Old World monkeys (Buttelmann, Carpenter, Call, & Tomasello, 2007; van de Waal & Whiten, 2012; Voelkl & Huber, 2000, 2007), as well as some species of birds (Akins & Zentall, 1996; Zentall et al., 1996).

Another method of identifying imitation of actions is through the Do-As-I-Do paradigm. This procedure requires an experimenter to first train an animal to

perform a number of actions on command. Subsequently, the trainer performs one of the trained actions, says "do this", and rewards an animal only if it performs the same action. This training procedure of action shaping and positively reinforced copying is repeated for a number of actions, and finally some novel untrained actions are introduced. An experimenter performs an untrained action and says "do this". The question is whether animals have learned to use this rule as a cue to imitate. If the animal copies a novel action, evidence of imitation has been found. This method has successfully identified imitative capacity in enculturated chimpanzees, orangutans, and dogs (Call, 2001; Custance, Whiten, & Bard, 1995; Topál, Byrne, Miklósi, & Csányi, 2006), but not capuchin monkeys (Fragaszy, Deputte, Cooper, Colbert-White, & Hémery, 2011). The incorporation of controlled and standardised procedures in the "Do-as-I-do" paradigm and two-action method have added empirical validity to less controlled examples of imitative behaviour in apes (Hayes & Hayes, 1952; Russon & Galdikas, 1993), and form the best available evidence of imitation in nonhuman animals.

Due to the correspondence problem, imitation is considered more cognitively demanding than other social learning mechanisms (Whiten, 2000), and conclusive identification of imitative learning in an experimental paradigm must rule out the possibilities of other simpler mechanisms giving rise to the

observed effect (Zentall, 2012). For example, after observing a conspecific cracking nuts with a nearby rock, a capuchin monkey might approach the conspecific and shortly afterwards, begin cracking nuts. A human observer recording this event might conclude that a monkey learned to imitate nut cracking behaviour. However, it could also be argued that the mechanism leading to the performance of the behaviour was local enhancement; the monkey was merely attracted to the site through the presence of the individual at the location, and the nut cracking behaviour was acquired through individual, trial-and-error learning (Heyes, Ray, Mitchell, & Nokes, 2000). Other mechanisms that could confound the study of imitative ability include stimulus enhancement (i.e. the animal is attracted to a specific object or stimulus type), affordance learning (i.e. the animal learns about the physical properties of an object), goal emulation (i.e. learning through observation of possible goals that can be achieved), and response facilitation (i.e. a behaviour already in an individual's repertoire is primed by observing the same behaviour being performed). In the past, the primary goal of social learning research was to isolate cases of imitation by using certain apparatus that prevents other non-imitative interpretations (e.g. the two-action method, see Dawson & Foss, 1965; or the ghost-apparatus, see Hopper, 2010), however, more recently there is a trend to examine other social learning mechanisms for their own sake.

It is encouraging that over the last decade promising steps have been made to develop a comprehensive understanding of social learning in nonhuman animals, examining numerous mechanisms (Amici, Aureli, & Call, 2013; Caldwell & Millen, 2009; Hoppitt, Blackburn, & Laland, 2007; Matthews, Paukner, & Suomi, 2010; McGuigan & Whiten, 2009), throughout a range of taxa (e.g. *Bombus terrestris*, Dawson, Avarguès-Weber, Chittka, & Leadbeater, 2013; *Drosophila melanogaster*, Sarin & Dukas, 2009; *Toxotes jaculatrix*, Schuster, Wöhl, Griebsch, & Klostermeier, 2006; H*omo sapien and Pan troglodytes,* Whiten, McGuigan, Marshall-Pescini, & Hopper, 2009). A thorough examination of simple mechanisms is crucial to the development of a comprehensive science of social learning in animals, and while it is recognised that a broad range of mechanisms play a role in social leaning (Caldwell & Whiten, 2002; Hoppitt & Laland, 2008a; Zentall, 2006), differentiating between mechanisms is different from understanding them (Galef, 2013). While convincing demonstrations of true imitation in nonhumans are rare, extensive evidence of other ways through which animals are influenced by the actions of conspecifics has been identified in a range of species.

Social contagion

Social contagion is defined as the "spread of affect, attitude, or behaviour from individual A (the initiator) to individual B (the recipient), where the recipient

does not perceive an intentional influence attempt on the part of the initiator''
(p 266, Levy & Nail, 1993). Social contagion is an umbrella term for a number of
different mechanisms, covering the transfer of emotional or motivational state
(e.g. fear, hunger), specific behaviours (e.g. yawning, scratching), or
behavioural states (e.g. play, locomotion). A number of specific terms have
been used to describe the social transmission of these various states, namely,
response facilitation, behavioural contagion, and emotional contagion (Hoppitt
& Laland, 2008). Response facilitation has been defined as the instances where
"the presence of a demonstrator performing an act (often resulting in reward)
increases the probability of an animal which sees it doing the same" (p. 237,
Byrne, 1994). Behavioural contagion has been described as a subset of response
facilitation where a class of behaviours are transmitted rather than one specific
behaviour, and the socially induced behavioural response is instinctual,
released without prior conditioned learning (Hoppitt & Laland, 2008; 2013).
While this distinction clearly outlines specific cases under which certain
terminology should be used, the study of socially transmitted behaviours of
this kind rarely differentiates between learned or innate response facilitation,
and in any case, this distinction is largely trivial. In most cases the prior
experience of an animal is unknown and it is impossible to identify whether the
socially transmitted behaviour is due to a learned or innate process. Therefore,
it has been argued that without detailed knowledge of an animal's
development, observations of behavioural transfer should be classified as

response facilitation rather than behavioural contagion (Amici et al., 2013; Hoppitt & Laland, 2008). However, this semantic distinction is rarely recognised. For example, it is well documented that the presence of another individual yawning increases the probability that an observer will yawn within-species (Anderson, 2010; Norscia & Palagi, 2011; Palagi, Leone, Mancini, & Ferrari, 2009; Platek, Critton, Myers, & Gallup, 2003), and between species (Harr, Gilbert, & Phillips, 2009; O'Hara & Reeve, 2011; Silva, Bessa, & de Sousa, 2012), and while this effect is almost ubiquitously referred to as behavioural contagion (e.g. Anderson, 2010; Platek et al., 2003), there is evidence that yawn contagion is not present from birth (Millen & Anderson, 2011), suggesting this phenomenon might more prudently be described using the more inclusive term of response facilitation.

Evidence of response facilitation is common in the comparative literature. Feeding and drinking behaviour is more likely to occur when others are feeding (Galef, 1993; Galloway, Addessi, Fragaszy, & Visalberghi, 2005; Hoppitt & Laland, 2008b; Visalberghi & Addessi, 2001). Yawning has received increasing interest, with evidence of within-species social facilitation in a number of primate species (Palagi et al., 2009; Paukner & Anderson, 2006; Provine, 1992), and dogs have also been found to yawn after seeing or hearing humans yawn (Joly-Mascheroni, Senju, & Shepherd, 2008; Silva et al., 2012).

15

Yawning is sometimes considered a form of displacement behaviour, and such displacement behaviours have also been the subject of much interest due to their contagious nature. Displacement behaviours are automatic behaviours, often self-directed and related to body-care or grooming (Troisi, 2002). Specific examples of these behaviours include scratching, or self-grooming in mammals (Cohen & Price, 1979; Maestripieri, Shino, Aureli, & Troisi, 1992), and preening in birds (Palestis & Burger, 1998). Similarly to yawning, preening and scratching behaviours are prompted by observing a conspecific perform the same behaviour (Feneran et al., 2013; Holle, Warne, Seth, Critchley, & Ward, 2012; Hoppitt et al., 2007; Palestis & Burger, 1998). The function of such socially facilitated behaviours is unknown, although in the case of scratching and grooming it could be related to awareness of parasite removal (see Chapter Six for further discussion on this topic). A separate line of research has identified a link between displacement behaviours and emotional arousal (Schino, Perretta, Taglioni, & Troisi, 1996; Troisi & Schino, 1987), which raises the question of whether emotional state may be contagiously transferred also, facilitating not only behavioural synchrony in a group but emotional synchrony.

If we observe socially facilitated behaviour we assume that some cognitive or emotional process, or a combination of the two, has instigated this behavioural change. It is sometimes useful to draw a distinction between these two

processes. While there will be some overlap between cognitive and affective mechanisms, the transfer of emotion is likely to incorporate the activation of unique neural and hormonal systems specific to emotion (Ledoux, 2000) that are known to have important short-term and long-term effects on behaviour (Katz, Roth, & Carroll, 1981) and physiology (Joëls et al. 2004). However, as it is difficult to assess the transfer of an emotional state between animals, emotional contagion, or emotional state-matching (de Waal, 2008) has been studied to a greater degree in humans. Behaviourally, observations of rapid mimicry of facial gestures has been proposed as evidence of emotional contagion in humans (Bourgeois & Hess, 2008; Hess & Blairy, 2001), and orangutans (Davila-Ross, Menzler, & Zimmermann, 2008). However, studies examining physiological measures provide clearer evidence of automatic emotional transfer. In humans, it has been found that observing someone experience anxiety or disgust elicits similar physiological responses in an observer (Buchanan, Bagley, Stansfield, & Preston, 2012; Waters, West, & Mendes, 2014; Wicker et al., 2003). These emotionally contagious responses are in some cases elicited in subtle ways. A participant watching the face of a second participant who is watching video clips showing actors displaying joy and fear reacts with corresponding facial expressions and exhibit increased skin conductance response (Dezecache et al., 2013). As behaviour is our primary window through which we can interpret an animal's emotions (Maestripieri et al., 1992), it is difficult to distinguish emotional contagion from behavioural contagion.

17

Displacement behaviours have been suggested as reliable indicators of emotional state (Maestripieri et al., 1992; Polizzi di Sorrentino, Schino, Tiddi, & Aureli, 2012), so when we see contagious displacement activity it is difficult to distinguish between a behavioural effect or an emotional phenomenon. This question has yet to be examined, and will be explored further in later chapters. Some have suggested that evidence of behavioural state matching, rather than the matching of specific behaviours *per se* qualifies as evidence of emotional contagion (Osvath & Sima, 2014). For example, upon seeing a conspecific playing, observer ravens will begin playing, however, the specific behaviours can be different (Osvath & Sima, 2014). Similarly, researchers examining contagion between different groups of captive primates have found that aggressive vocalisations from one primate group tend to increase aggressive behaviours in neighbouring groups (Grand & Leighty, 2013; Videan, Fritz, Schwandt, & Howell, 2005; Watson & Caldwell, 2010). Affiliative emotional contagion seems to take place when more affiliative vocalisations are heard (Videan et al., 2005; Watson, Buchanan-Smith, & Caldwell, 2014; Watson & Caldwell, 2010). These neighbour effects are some of the best evidence we have of emotional contagion in nonhuman animals as the vocalisations that elicit behavioural responses match the actions they produce in terms of emotional content, but not with regard to the specific behavioural responses. However, further experimental work is necessary to gain a complete understanding of the

interaction between behavioural and emotional contagion (as outlined in Chapter 4).

Learning from products

Having examined how a conspecific's actions can influence the behaviour of an observer, the influence of the products of those actions will now be explored. When learning from the products of behaviour an observer does not learn from or about a motor action. Instead, by observing a conspecific's behaviour, individuals might learn something about the environment. An animal might learn how something in the environment works (i.e. affordance learning), or that a certain goal is possible (i.e. goal emulation), or more attention might be paid to a specific location or stimulus (enhancement effects). During social learning of this type the motor action of the observed individual has no direct effect on the motor action of the observer (as is the case during behavioural contagion or imitation), however, a shared goal, or shared attention, can have the result of producing matched behaviour. Some of the mechanisms described in this section are considered simple in terms of the cognitive processing required, especially when compared to some forms of imitative learning (i.e. compare the associative account of enhancement effects, Leadbeater, 2015, with the hierarchical model of imitation, Byrne & Russon, 1998). However, these learning effects have been observed in a diverse range of species and likely play

a significant role in the lives of many species.

Enhancement effects: The stimulus and the location

If observing an animal interact with a stimulus increases the likelihood of observers interacting with that same stimulus at a later time, stimulus enhancement is thought to have occurred (Hoppitt & Laland, 2013). If observing an individual in a certain location increases the likelihood that an observer will spend time in that location, local enhancement is argued to have taken place (Hoppitt & Laland, 2013). Some have considered local enhancement to be a special case of stimulus enhancement where the location acts as the stimulus (Galef, 1988; Heyes, 1994). However, Hoppitt and Laland (2013) prefer to differentiate between the two mechanisms and propose that different cognitive processes will produce distinct behaviour in each instance. For example, stimulus enhancement is said to operate as a social case of single-stimulus learning (Heyes, 1994; Hoppitt & Laland, 2013). Single-stimulus learning is a basic principal of learning theory where the presence of a stimulus acts to make an animal more or less responsive to that stimulus at a future time; these effects are known as sensitisation and habituation respectively (Heyes, 1994). During stimulus enhancement, an individual is thought to become sensitised to a stimulus after observing a conspecific interact with it, subsequently increasing the rate of interaction with that stimulus. However,

during stimulus enhancement, learning is not limited to a single stimulus, but this increased sensitivity becomes generalised to other stimuli that share some sensory feature (Hoppitt & Laland, 2013); this is not thought to occur with local enhancement. Local enhancement does not act to sensitise an observer to a given location, but instead draws an individual to that location for other reasons that may not necessarily persist at a future time (i.e. an individual might be attracted to a location for social bonding, or to group with others for warmth; Hoppitt & Laland, 2013). The difference between these enhancement effects is the type of learning that takes place. During stimulus enhancement something is learned about a stimulus that changes behaviour at a future time, but during local enhancement an animal is drawn towards a location because of a conspecific's presence; learning may take place at that location but the act of local enhancement is not itself an instance of learning about a location. Local enhancement by this definition serves to describe a different phenomenon to stimulus enhancement.

Occasionally, evidence of enhancements effects is discovered while studying imitation or general social learning ability in animals (Caldwell & Whiten, 2004; van de Waal & Bshary, 2011; Wilkinson, Kuenstner, Mueller, & Huber, 2010). For example, common marmosets (*Callithrix jacchus*; Caldwell & Whiten, 2004) and keas (*Nestor notabilis*; Huber, Rechberger, & Taborsky, 2001) who had

observed conspecifics interacting with an apparatus did not imitate the specific behaviour of the models, but did interact more often with the elements of the apparatus that models touched. Studies specifically aimed at examining stimulus and local enhancement have found examples in a range of species. Ninespined stickleback (*Pungitius pungitius*) are more likely to feed in a location where a conspecific was observed feeding, but do not generalise this learning to other stimulus types (e.g. colour; Webster & Laland, 2012). A later study by the same authors (2013) found that male guppies (*Poecilia reticulata*) were attracted to the location where other males were performing mating displays, but only when those models were present at the location. If the demonstrating male was removed before the observers were allowed to make their decision, no local enhancement effect was found (Webster & Laland, 2013).

Some believe that associative learning processes may determine local enhancement (Leadbeater, 2015), and given that both single-stimulus learning and associative learning are evolutionarily ancient it is not surprising that evidence of enhancement effects have been reported in invertebrates, amphibians, and reptiles. Gregarious locusts (*Schistocerca gregaria*) prefer to lay eggs and feed near conspecifics (Lancet & Dukas, 2012). After observing conspecifics in a specific part of a water tank, wood-frog tadpoles (*Lithobates sylvaticus*) will move to that location even after the conspecifics are no longer at

that location (Chapman, Holcomb, Spivey, Sehr, & Gall, 2015). Moreover, even non-social animals, like insular lizards (*Podarcis lilfordi*), prefer to feed near conspecifics (Pérez-Cembranos & Pérez-Mellado, 2014). Even when learning does not occur during local enhancement, being near a conspecific may influence behaviour in other ways. Hoppit and Laland (2013) suggest that animals that congregate may tend to be coordinated in their feeding and foraging behaviours, especially under patchy feeding conditions. This may explain evidence of behavioural synchrony in baboon troops that travel together through varying environments (King & Cowlishaw, 2009), and may drive shared decision making when travelling through an environment (Strandburg-Peshkin, Farine, Couzin, & Crofoot, 2015).

Some recent studies have attempted to differentiate between types of enhancement. While differentiation is sometimes based upon whether the cue that facilitated learning was spatial or not (Guillette & Healy, 2014; Mersmann, Tomasello, Call, Kaminski, & Taborsky, 2011), some studies do attempt to tease apart whether learning has generalised to other stimuli, indicative of stimulus enhancement rather than local enhancement. One study found that bees (*Bombus terrestris*) that had associated live conspecifics with rewarding flowers would subsequently use fake social cues (i.e. model bees placed on flowers of a certain colour) to determine the colour of flower on which to forage (e.g.

stimulus enhancement; Avarguès-Weber & Chittka, 2014). However, bees that in an initial stage had learned to associate model bees, rather than live conspecifics, with rewarding flowers were found at the second stage of testing to only favour foraging on flowers where model bees were present without showing a preference for a colour of flower. While this study demonstrates that previous experience contributes to social learning processes, the authors conclude that the difference observed between social and non-social conditions also suggests that some evolved capacity may explain differences between individual and social learning.

In recent years there has been an important drive to understand more about the mechanisms that facilitate social learning in animals, and importantly, evidence of simpler enhancement effects are now being investigated in earnest to learn about what conditions are necessary for learning to occur (e.g. Webster & Laland, 2013) and what types of previous experience may be necessary to facilitate these effects in the first place (Avarguès-Weber & Chittka, 2014; Dawson et al., 2013). Evidence that enhancement effects are widespread throughout a range of animal taxa may lead to the conclusion that complex patterns of behaviour only observed in some species (e.g. social traditions) cannot be a result of these mechanisms. However, recent evidence suggests otherwise. Stone handling behaviours thought to be an example of a cultural

tradition in Japanese macaques (*Macaca fuscata*; Huffman, 1996) have recently been found to be facilitated by "simple" enhancement effects (Leca, Gunst, & Huffman, 2010). Beyond enhancement effects there are other ways in which the products or results of behaviour may influence others, and these will be explored next.

Emulation

The term emulation has a number of meanings in the comparative and developmental literature. Hopper (2010) distinguishes between three forms of emulation: Goal emulation, affordance learning, and object movement re-enactment. Goal emulation takes place when after observing another individual complete an action that produces some measurable result (e.g. a food reward), the observer is motivated to achieve the same goal, but may do so by different means (Call & Carpenter, 2002; Hopper, 2010; Whiten & Ham, 1992). An example of this type of goal emulation was observed by Tomasello and colleagues (1987) who found that after observing a conspecific use a tool to obtain a food reward, chimpanzees were more likely to use the same tool to gain the reward, even though the observers used different actions. The authors believe that chimpanzees were motivated to use the tool to achieve the same goal (i.e. achieve a food reward) but the specific method to achieve this reward was acquired through individual learning. Stimulus enhancement was ruled

out in this instance as chimpanzees that had not seen a demonstrator were just as likely to interact with the tool but they did not use it to get a food reward.

Affordance learning is influenced by the ecological psychology of J. J. Gibson who defined affordances as what an environment or object offers an animal (1977). For example, a horizontal, flat, rigid, and extended surface affords *support*; a surface with these properties and located at knee height affords *sitting* (Gibson, 1977). Any object in an environment could afford any number of manipulations or actions, however, some affordances are not readily available through simple observation. For example, a nut with a shell may afford *cracking* but this information is not available purely by observing the nut. An individual might learn that certain nuts afford cracking through trial and error learning, but this may also be learned by observing another individual crack a nut. Finally, through object movement re-enactment (OMR), an individual might learn about the way in which an object might move (Hopper, 2010). In many cases "ghost procedures" have been employed to distinguish imitation from OMR. Studies that use ghost procedures compare individuals who have observed a demonstrator successfully manipulate an apparatus to gain a reward, with individuals who have seen the apparatus being manipulated by hidden pulleys or strings, without a demonstrator present (i.e. the ghost demonstration). If observers learn to operate the apparatus after observing the

ghost demonstration then OMR is said to have occurred rather than imitation (Hopper, Lambeth, Schapiro, & Whiten, 2008; Hopper, 2010). These three types of emulation learning are in many cases difficult to differentiate, as the behaviour observed after all three cases of learning will often be the same (Hopper, 2010). Evidence of emulative learning is less common than enhancement effects. A number of studies report evidence of learning from emulation in children (Hopper et al., 2008; McGuigan & Whiten, 2009; Tennie, Call, & Tomasello, 2006), however, opinions differ regarding its relative significance to social learning in apes (Hopper et al., 2008; Tennie et al., 2006; for a review see Byrne, 2002a).

While it is interesting to differentiate between imitative learning and emulation learning, it is also important to recognise that emulative learning may be as important as imitation in driving complex behaviour in humans. For example, Caldwell and Millen (2009) examined social learning in humans by manipulating the amount of information a learner received. The task's goal was to create a paper aeroplane that could fly as far as possible. In one condition participants could observe others make their paper aeroplane (i.e. learning from actions) while in another condition participants could only see the finished paper aeroplane with information on how far it flew (e.g. learning from an end-state and goal). In both cases, social learning occurred,

demonstrating evidence of both emulative and imitative learning. Furthermore, this study incorporated a transmission-chain method which simulated human cultural practices, allowing the transfer of previously learned skills to a new "generation" of participants (whether through actions or products). It was found that performance improved over generations (i.e. aeroplanes flew further) providing evidence of cumulative culture (the capacity for learning to improve cumulatively over generations). Interestingly, cumulative learning occurred in both imitative and emulative conditions suggesting that end-state matching and goal emulation can under some circumstances help drive a phenomenon thought to be a cornerstone of human cognition.

Learning from presence

In some cases, it is not the behaviour of a conspecific, nor the results of behaviour that influence an observer. Sometimes, an animal's presence is enough to affect behavioural or motivational change in another. Nothing is learned during presence effects, but they are an important category of mechanism to understand, especially in the context of how they interact with other social learning mechanisms. The main mechanism to be considered here is social facilitation, but the effect of group size on behaviour will also be examined.

Social facilitation

Zajonc (1965) differentiated between two types of social facilitation: Audience effects and co-action effects. Audience effects are limited to events where the mere presence of another individual (or individuals) has the effect of changing behaviour. This definition is in line with contemporary usage of social facilitation (e.g. Hoppitt & Laland, 2013). Co-action effects, on the other hand, occur when individuals in groups are simultaneously engaged in the same behaviour (Zajonc, 1965). Social facilitation as co-action will not be discussed here as it does not contribute further insight to the study of social learning mechanisms once contagion effects or two-way audience effects are considered. Audience effects have been studied in experimental conditions where it has been discovered that behaviour is significantly altered by the presence of another individual (for reviews see Aiello & Douthitt, 2001; Zajonc, 1965). Generally, it is found that well-established behaviours that are easy to execute are performed more often as a result of audience effects while newly learned behaviours or behaviours that require greater cognitive effort are inhibited (Zajonc, 1965). For example, on simple tasks that test a participant's attention, eye-hand co-ordination, or reaction time, humans perform better when someone else is nearby (Bergum & Lehr, 1963; Travis, 1925). However, less automatic responses are often inhibited by an audience. Zajonc and Sales (1966) employed a clever method to examine audience effects on easy and difficult tasks. Initially, American participants were trained to pronounce

different Turkish words, but the training was unequal and participants received a lot of training for some words and very little for others. In a testing phase, the trained words were flashed upon a screen for a very short period of time (1/100th second) and participants were asked to pronounce the words they observed. Overall, rapid stimulus presentation led to poorer recall for words that had received little training, and greater recall for words that had received considerably more training. However, comparing audience effects for over-trained words and under-trained words, researchers found that when it came to over-trained words performance was better with an audience present, while the opposite effect was found for under-trained words. Evidence of social facilitation is not limited to humans, with the presence of a conspecific increasing the rate of bar pressing in rats and macaques (Levine & Zentall, 1974; Reynaud, Guedj, Hadj-Bouziane, Meunier, & Monfardini, 2015). Social facilitation effects have also been observed in feeding contexts where the presence of others influences food intake. Humans eat more and have longer meals when eating with others (Decastro, 1994), and chicks raised in pairs eat more than those raised in isolation (Tolman, 1964).

Zajonc (1965) explains social facilitation as increasing the "drive" (i.e. psychological and physiological arousal) of an individual leading to improved performance on simple tasks. However, a recent study identified greater

activity in brain regions related to attention in monkeys during tasks conducted in the presence of a conspecific, but no increase in brain regions related to motivation and no change in stress hormone levels (Monfardini et al., 2015). This study provides some insight into the physiological basis of social facilitation, but no support for Zajonc's theory of increased "drive".

Group-size effects

This final mechanism is not regularly included in the taxonomy of social learning processes, possibly because it could be considered a special case of social facilitation (e.g. Meunier, Petit, & Deneubourg, 2007). Nonetheless, research has demonstrated that the number of conspecifics present at a given time influences behaviour, so it is important to consider group size when discussing presence effects. Also, the number of conspecifics present at an area can lead to behavioural change unrelated to audience effects; for example, a larger group may facilitate increased foraging rates due to shared vigilance to predators. In fact, the effect of group size has mostly been studied in the context of vigilance in birds, primates, and other mammals (Beauchamp, 2012; Lazarus, 1978; Pays et al., 2009; Robinette & Ha, 2001; Treves, 1999). It is believed that one of the benefits of group living is that increased total vigilance in groups helps avoid predation (Lazarus, 1978). Indeed, in many studies of group-living animals we find that as group size at a given time increases, the proportion of

individuals scanning their surroundings is reduced (Ebensperger, Hurtado, & Ramos-Jiliberto, 2006; Lazarus, 1978). Measures of collective vigilance have been found to increase as group-size increases while individual vigilance decreases (Ebensperger et al., 2006) and may facilitate more varied foraging strategies (Beauchamp, 2013). Interestingly, when this effect has been studied in primates the opposite relationship has been observed. As group-size increases in primates the number of individuals showing vigilant behaviour also increases (Hirsch, 2002; Kutsukake, 2007; Robinette & Ha, 2001; Treves, 1998). It is thought that this may be caused by a need to detect threats of aggression or scrounging from conspecifics rather than vigilance for predators (Hirsch, 2002) and has been observed in at least one other large brained non-primate species (*Corvus caurinus*, Robinette & Ha, 2001). Group-size effects may also indirectly contribute to a variety of other social learning mechanisms, as greater numbers of individuals increase the possibility of any social learning, whether via response facilitation, imitation, emulation, or audience effects.

Social learning from the bottom up

It is useful to delineate the contexts under which social learning takes place. However, the naming of mechanisms and distinguishing between specific mechanisms is only the beginning of understanding the science of social learning. Over a decade ago, Byrne (2002b) highlighted that while it is certainly

beneficial to describe the various social learning mechanisms (e.g. Hoppitt &

Laland, 2008; Whiten & Ham, 1992; Zentall, 2006), this approach tends to focus

on the form of the behavioural phenomena observed and not on how the

mechanism might operate or how it may develop. It seems that little progress

has been made in this regard, as more recently Galef (2013) has similarly

endorsed the idea that while definitional consensus is useful, it may

inadvertently restrict the scope of social learning research. Galef argues that the

methods used to identify social learning (notably the two-action method, i.e.

Dawson & Foss, 1965) have not contributed to understanding the cognitive

processes underlying social learning but instead merely differentiate between

imitative learning and other "simpler" flavours of social learning. As the field

of social learning research has progressed over the last two decades a general

consensus has emerged concerning the description of the behavioural

phenomena covered by scientists of social learning, and these include the

definitions detailed above. The greatest debate concerning ways of

discriminating between mechanisms have been retained for those processes

considered the most complex, namely imitation and emulation (see Caldwell &

Whiten, 2002). Often, simple processes are explored as mere alternative

explanations once imitative learning is ruled out, but Galef argues that the

consensus concerning these definitions have been mistaken for understanding

these simpler mechanisms. We may agree that stimulus enhancement, for

example, takes place when a conspecific's interaction with a certain stimulus

influences an observer to pay closer attention to, or interact with that stimulus. However, we know little about the cognitive mechanisms that underlie this phenomenon, how this cognitive ability develops in an individual, how it is phylogenetically distributed, or what internal states and external stimuli facilitate or disrupt the process. According to Galef, a lifetime of work awaits those interested in answering these questions on the simpler processes that are likely to influence behaviour in a wide range of species. In this thesis I aim to in some way address this need by focusing on these simpler processes, examining how they may function and develop in primates.

Having identified a problem, it is necessary to consider an approach that might afford a better understanding of the cognitive processes involved in social learning. In recent years, some comparative psychologists have expressed an interest in tackling animal cognition from the bottom up. de Waal & Ferrari (2010) highlight the trend in animal cognition research, especially in the field of primatology, to focus on cognitive processes we might think are uniquely human, like mental time-travel (Vale, Flynn, & Kendal, 2012), empathy (Preston & de Waal, 2002), and imitation (Whiten & Ham, 1992), in an effort to discover evolutionary homologues in our primate relatives. An approach to animal cognition concerned with exploring complex cognition from a top-down perspective asks: "can this species perform this complex cognitive task?", with

a null result forcing us to instead consider simpler mechanisms as alternative explanations for the observed behaviour. This approach has been criticised for taking an anthropomorphic stance to animal cognition (Barrett, Henzi, & Rendall, 2007; Shettleworth, 2010), and instead it has been argued that a greater understanding of the simpler processes that underlie or scaffold more complex cognition will deliver a more thorough comparative approach to cognition (de Waal & Ferrari, 2010). For example, before empathy is questioned, the mechanisms that facilitate empathy should be explored (e.g. emotional contagion, Preston & de Waal, 2002). To understand imitation we must understand the role of mirror neurons in action matching (de Waal & Ferrari, 2010). Other researchers are similarly motivated to dissect the cognitive capacities of animals from the ground-up. Shettleworth (2010) has argued that the focus on identifying cognitive mechanisms in other animals that resemble human processes misses opportunities to explore the more simple or automatic processes that will underlie both human and animal behaviour. Shettleworth specifically references evidence of a preference for immediate pay-off over more long-term rewards that is common in both humans and many other species (Anderson, Kuroshima, & Fujita, 2010; Frederick, Loewenstein, & O' Donoghue, 2002; Vick, Bovet, & Anderson, 2010). The idea that a quick, automatic, domain-general, and evolutionarily ancient cognitive and emotional system underlies much of human behaviour has gained considerable interest in other fields (Damasio, 1996; Kahneman, 2011). This reinterpretation of the goal

of comparative psychology drives the research program outlined in this thesis. Complex cognitive abilities may exist in both humans and nonhuman animals but a complete picture of these processes will not be gained by approaching these abilities from the top. In the field of comparative social learning the top has traditionally meant imitation, but some recent empirical and theoretical work suggests that starting at the bottom may be a more fruitful enterprise.

An associative account of social learning

The study of social learning mechanisms has greatly benefited from a largely consensual view of the mechanisms of social learning, however, there is still much to learn about the basic processes involved for each mechanism described. Under the cognitive paradigm behaviourist principles have fallen out of fashion, labelled as "killjoy" explanations (Dennett, 1983) that incorporate "awkward terminology" (Tomasello, 1998), but the tenets of associative learning are largely misunderstood (Barrett, 2011b; Rescorla, 1988), and can contribute greatly to an understanding of social learning. Some steps have already been taken to examine the role of associative processes in social learning.

A comparative science of social learning suffers from a habit of setting out to identify some variety of social learning in an animal, without asking questions

about how specific types of social learning may have developed and how they may work. In the field of primate research the ontogeny of a social learning mechanism is difficult to assess as most long-lived primates lead rich social lives before ever interacting with a two-action apparatus. It is not surprising then that much of the research concerned with the development of social learning mechanisms comes from organisms whose life-history is easier to control. Some studies with invertebrates have highlighted the importance of previous experience to exploit social information adaptively (Avarguès-Weber & Chittka, 2014; Dawson et al., 2013).

Where bumblebees (*Bombus terrestris*) have learnt to associate conspecifics with rewarding flowers, they will subsequently be attracted to flowers where they observe conspecifics. Conversely, where bees have learned to associate conspecifics with unrewarding flowers, they will use a conspecifics presence to avoid that flower (Dawson et al., 2013). This demonstrates that simple associative processes are responsible for at least some social learning processes. More recently, it was found that after learning to associate live conspecifics with rewarding flowers, subsequent observations of model bees on flowers of a certain colour led the bees to forage on all flowers of that colour (evidence of stimulus enhancement- see above; Avarguès-Weber & Chittka, 2014). However, learning to associate model bees and rewarding flowers facilitated subsequent

foraging only at sites where models bees were located; in other words learning was not generalised to other flowers of the same colour (evidence of local enhancement; Avarguès-Weber & Chittka, 2014). The authors conclude that while some forms of social learning are facilitated by simple associative processes (e.g. local enhancement), some innate mechanism may be required to bring about stimulus-enhancement effects. This may be the case, but the authors do not address olfactory cues available to bees during social training that may facilitate associative learning even when visual cues are absent. Nevertheless, the fine-grained teasing apart of differences between social and non-social associations, as well as the insight gained from examining the role of previous experience, demonstrates how little is known of how simple mechanisms operate. Associative processes have been used to explain enhancement effects (Leadbeater, 2015), but recent research has also examined the role of associative processes when learning from actions.

An associative account of action imitation has been proposed (Heyes & Ray, 2000). From this perspective, a motor representation of an action (e.g. a hand opening) becomes associated with a sensory representation of that action (e.g. observing a hand opening) through any contiguous and contingent sensory-motor experience. Once an association has developed, the sensory experience of an action may activate the motor representation of that action and lead to a

matching action response. While this type of sensorimotor experience can occur through self-observation, it also takes place when animals are performing the same behaviour in synchrony. For example, a group of chickens foraging together may begin pecking when a food source becomes available. During this feeding event an individual may develop an association between the action of pecking and the sensory experience of seeing conspecifics peck. In this example, the sensory-motor association will also become associated with the presence of food, which may act to strengthen this association. After this sensorimotor experience, future observations of pecking may cause an observer to peck. In fact, previous studies have found that pigeons will imitate both pecking and stepping actions (Zentall et al., 1996), potentially facilitated by past sensorimotor experience. This associative model was proposed to explain how animals may solve the correspondence problem (Heyes & Ray, 2000), but similar Hebbian models at the neurological level have been proposed to explain action imitation and action understanding (Del Giudice, Manera, & Keysers, 2009; Keysers & Perrett, 2004; although see Catmur, 2011, for important differences). This associative approach to imitation has also been extended to account for the development of mirror neurons (Cook, 2012; Heyes, 2010), and importantly, is supported by studies that have tested the predictions of this model in the context of action imitation (Gillmeister, Catmur, Liepelt, Brass, & Heyes, 2008; Press, Gillmeister, & Heyes, 2007) and mirror neuron function (Catmur, Mars, Rushworth, & Heyes, 2011; Catmur, Walsh, & Heyes, 2007).

While associative accounts of behaviour may not be in vogue in the current cognitive climate, it is important to test their validity. The potential of these associative models lies in their ability to predict behaviour in humans and other animals, and while some have criticised the generalisability of associative models to more complex forms of social learning (Gallese, Gernsbacher, Heyes, Hickok, & Iacoboni, 2011; Rawlins et al., 2005), it is important to consider how these models might explain aspects of social learning processes before turning to explanations that require top-down processing or richer representational accounts.

A better understanding of social learning processes can be gained from a study of associative accounts of social learning, and so-called "simple" mechanisms of social learning are worthy of consideration in their own right. The answers gained from taking this bottom up approach will contribute to a deeper understanding of social learning in human and nonhuman animals.

Thesis goals

Having summarised the state of social learning research in the field of comparative psychology and highlighted the broader theoretical and empirical problems in this area, I will now outline how the studies forming the backbone

of this thesis address these issues. Four of the five data-chapters to follow examine the cognition, behaviour, and physiology of capuchin monkeys (*Sapajus sp.*). Capuchin monkeys are a New World species that interest researchers of social learning because of their high brain to body-mass ratio (Macphail, 1996), socially tolerant nature (Fragaszy, Feuerstein, & Mitra, 1997), tool use capacities (Visalberghi, 1993), and evidence of socially learned traditions in wild populations (Perry, 2011). Capuchins have been studied extensively to examine their social learning abilities (Dindo, Thierry, & Whiten, 2008; Dindo, Whiten, & de Waal, 2009a; Fragaszy et al., 2011; Visalberghi & Addessi, 2001) yet no evidence of action imitation has been identified in this species (Fragaszy & Visalberghi, 1989; Fragaszy et al., 2011). Here, a bottom-up approach to social learning will examine the prevalence of other, simpler social learning mechanisms in capuchins and their role in capuchin behaviour.

In Chapter Two, action imitation will be examined in the context of a stimulus-response experimental paradigm. While previous studies have failed to identify action imitation in capuchins, this study examines any bias towards imitating actions using a novel method for the first time with non-human primates. Using a stimulus-response method allows the testing of predictions made by an associative account of action imitation and facilitates testing of the role of sensorimotor experience in action imitation. Chapter Three further develops the

study of an associative account of action imitation but with human children. The study reported in Chapter Three complements the study of action imitation in capuchins by examining the same associative principals introduced in Chapter Two. Chapter Four returns to capuchin monkeys to examine a range of social mechanisms that have been underexplored in the primate literature. Using observational methods, capuchin behaviour is studied at the group level allowing a thorough examination of the factors that might influence group behaviour in capuchins. The focus of this chapter is to address phenomena that are under-explored in the primate literature, namely, group-size effects, behavioural synchrony, and inter-group social contagion. Chapter Five examines emotional contagion. While thought to be the foundation of empathy, this topic is difficult to study in primates as behavioural measures of emotion are difficult to validate. Here, an experimental paradigm allows the measurement of both behaviour and stress hormone levels to examine the impact of emotionally valenced stimuli on the emotional response of capuchins. The physiological measurement of stress also allows the validation of behavioural measures of emotional states in capuchin monkeys. The phenomenon of behavioural contagion is examined further in Chapter Six. This chapter specifically addresses a behaviour that is contagious in primates but is also linked to emotion in primates: Scratching. Together these studies shed light on some of the lesser studied mechanisms of social learning, and provide a better understanding of the factors that contribute to social learning.

Chapter 2: Automatic imitation in capuchin monkeys

During social interactions we unconsciously adopt each other's behavioural tics, imitate actions, and synchronise our postures. We prefer individuals that imitate us (Chartrand & Bargh, 1999), and act more prosocially following these interactions (Stel, Van Baaren, & Vonk, 2008). This phenomenon, dubbed the chameleon effect, has understandably garnered much interest from social psychologists since its discovery over a decade ago (Chartrand & Bargh, 1999; Stel et al., 2008; van Baaren, Janssen, Chartrand, & Dijksterhuis, 2009). Meanwhile, a similarly unconscious and automatic effect has been identified in controlled cognitive studies. Seeing an action (e.g. opening a hand) primes the performance of that action but interferes with the execution of an incompatible action (e.g. making a fist). Automatic imitation is a reliable behavioural effect, specifically related to motor imitation, and distinct from other stimulus-response compatibility effects (Boyer, Longo, & Bertenthal, 2012; Catmur & Heyes, 2011). Examining automatic imitation, cognitive neuroscientists have been asking what this phenomenon might reveal about imitative learning in humans (Brass, Bekkering, & Prinz, 2001; Capa, Marshall, Shipley, Salesse, & Bouquet, 2011; Cook, Press, Dickinson, & Heyes, 2010; Heyes, Bird, Johnson, & Haggard, 2005).

We can imitate by recreating, through action, the perceived visual qualities of the act we see performed by another. However, the visual information obtained from perceiving someone perform an action often does not correspond to the sensory experience of observing your own actions (for a more detailed discussion on this problem see Chapter One). This is especially problematic when the nature of the action renders it opaque to the actor (e.g. in the case of facial gestures). Mirror neurons, first discovered in the F5 region of a pigtailed macaque's parietal lobe by researchers in Parma (di Pellegrino, Fadiga, Fogassi, Gallese, & Rizzolatti, 1992; Rizzolatti, Fadiga, Gallese, & Fogassi, 1996), may offer an explanation for the ability to solve this "correspondence problem" (Nehaniv & Dautenhahn, 2002). Neurons sampled in this premotor area fired when the macaque performed an action (i.e. grasping a peanut), and also when the monkey observed the researcher perform the same action. These initial studies described neurons with both visual and motor properties, single cells that could represent information about another's actions in egocentric terms. A thorough exploration of this neural subset was published in 1996, outlining multiple properties of these cells, referred to for the first time as "mirror neurons" (Gallese, Fadiga, Fogassi, & Rizzolatti, 1996). For example, these neurons fired when monkeys observed an experimenter acting upon an object but did not fire when the object or the action were presented in isolation. While most neurons were active for specific motor actions (i.e. a power grip or precision grip), some neurons were sensitive to the goal of the action, firing

irrespective of effector (i.e. three sampled neurons fired when the experimenter picked up an item using either the hand or mouth). Subsequent studies of single neurons have explored interesting properties of these macaque mirror neurons (see Caggiano, Fogassi, Rizzolatti, & Thier, 2009; Keysers et al., 2003; Umiltà et al., 2001), and studies suggest a comparable system exists in humans (Hari et al., 1998; Iacoboni et al., 1999; Mukamel, Ekstrom, Kaplan, Iacoboni, & Fried, 2010).

The function of these neurons has been disputed (see Gallese, Gernsbacher, Heyes, Hickok, & Iacoboni, 2011, for a forum discussion), but a parsimonious interpretation suggests mirror neurons play a role in recognising the actions of others (Bonini & Ferrari, 2011; Gallese et al., 2011). Importantly, while the primary function of mirror neurons may not be related to imitation, through action recognition, these neurons could still solve the correspondence problem by recruiting additional brain regions. Function aside, the origin of mirror neurons, the question of whether these neurons are innate or formed through experience, deserves consideration.

Mirror neurons have understandably received a great deal of attention and two explanations for how these neurons came to exist in primate brains have been

proposed. One account suggests mirror neurons have evolved for the specific purpose of solving the corresponding problem, and exist from birth as an adaptation. Heyes (2010) points out that this approach is implicit in many discussions of mirror neurons and imitative learning (e.g. Meltzoff & Moore, 1997; Rizzolatti & Arbib, 1998). A competing view proposes mirror neurons develop through experience, and are not present at birth (Heyes, 2010). Both models were originally proposed to explain imitation but have subsequently been refined and adapted to account for mirror neuron function (Catmur, Walsh, & Heyes, 2009; Heyes, 2010; Meltzoff, 2005). For example, the active intermodal mapping account (AIM) describes an innate process that matches the representation of observed motor actions with proprioceptive feedback from the performance of the same action (Meltzoff & Moore, 1997; 1983). Support for the AIM account is provided by reports of imitation in infants too young to have learned to imitate from experience of social interaction (Meltzoff & Moore, 1977, 1983). An alternative theory, first outlined by Heyes and Ray in 2000, favours an associative, developmental approach to imitation (for a more detailed recent account see Cook, Bird, Catmur, Press, & Heyes, 2014). The associative sequence learning (ASL) approach posits imitative ability (and a mirror neuron system) is formed through compatible sensorimotor experience, the contingent experience of performing and observing the same action (Heyes, 2010; Ray & Heyes, 2000). This sensorimotor experience could occur when an infant observes their hands, (Del Giudice et al., 2009), or by being imitated by

caregivers. It has been shown that during interactions between mothers and young infants (17-33 weeks of age), 16% of the time was taken up with the mother imitating the child (Pawlby, 1977). Heyes and her colleagues suggest this type of interaction is essential for learning an association between the sensory and motor properties of an action, creating sensorimotor, neural connections through Hebbian processes (Cook et al., 2014; Heyes, 2010; Ray & Heyes, 2011b). Importantly, we can test predictions made by these approaches to better judge their validity.

While a number of studies have reported evidence of neonatal imitation (Meltzoff & Moore, 1997, 1983; Meltzoff, 1988), the generalisability of this effect has been questioned (Anisfeld, 1996; Hayes & Watson, 1981; Lodder et al., 2014; Ray & Heyes, 2011b). It has been reliably discovered that infants imitate tongue protrusion actions (e.g. Meltzoff & Moore, 1983; Soussignan et al., 2010; for reviews see Anisfeld, 1996; Ray & Heyes, 2011), however, this behaviour is also elicited by flashing lights and music (Jones, 1996; Jones, 2006). These supplementary findings lend support to the idea that tongue protrusion is an innate exploratory behaviour elicited by multiple arousing stimuli, ungoverned by innate intermodal processes (Anisfeld, 1996). For example, upon finding that a variety of non-social stimuli elicited tongue protrusion in neonates, Jacobson (1979) proposed that these observations make sense when stimuli could be

interpreted in the context of a feeding event (e.g. resembling a nipple). However, criticisms of neonatal imitative effects have been countered by recent suggestions that null results may be due to type II errors (Simpson, Murray, Paukner, & Ferrari, 2014). Simpson and colleagues (2014) extracted relevant data concerning effects sizes and samples sizes from studies that have found an effect of neonatal imitation, concluding that a sample size of 26 individuals is necessary to identify neonatal imitation (when power = .80, α = .05, f = 0.4). The authors demonstrate that studies that met this sample-size criterion were more likely to discover neonatal imitation effects while studies that report null effects were more likely to have lower sample sizes. Nonetheless, as recent research suggests early experience is important for the development of imitative ability (de Klerk, Johnson, Heyes, & Southgate, 2014; Vanderwert et al., 2015) it is far from certain that precocious imitative ability is necessarily indicative of innateness.

While the best evidence supporting an innate action matching mechanism is debatable, increasing support for the ASL view has been provided by examining the manipulation of automatic imitation in stimulus-response compatibility (SRC) tasks. In an SRC task participants are asked to perform two different actions (e.g. hand opening/closing) in response to releasing stimuli (words, colours, etc.). A task irrelevant image that is either action compatible or

action incompatible accompanies the stimulus. Reaction times are consistently quicker when the image presented corresponds with the action to be performed, while incompatible images invoke slower responses (Brass et al., 2001; Brass, Bekkering, Wohlschläger, & Prinz, 2000; Heyes et al., 2005; Stürmer, Aschersleben, & Prinz, 2000). If imitation is dependent on sensorimotor experience, automatic imitation effects could be easily eliminated through incompatible sensorimotor training (where images of incompatible actions are repeatedly paired with releasing stimuli). Indeed, an incompatible training session delivered 24 hours before a test of automatic imitation significantly reduced the effect (Heyes et al., 2005). Catmur et al. (2008) using a similar method examined activity in brain areas associated with mirror neuron activity in humans. After incompatible training (performing hand actions when presented with an image of a foot and vice versa), brain areas previously related with hand actions were active when viewing images of a foot.

It is worth noting that while I have focussed on the ASL approach here, another domain-general account of imitation has also been proposed. Prinz (1997; 2005) has described how psychological research throughout the 20th century focused on a sensory-motor paradigm, considering action as the result of stimuli. An ideomotor approach presents action as the result of intention, a potentially fruitful alternative to the dominant paradigm, and a useful theoretical tool for

the study of imitation (Prinz, 2005). The ideomotor approach suggests that sensory and motor representations are not only encoded separately but are also cognitively linked (i.e. this is known as dual coding; Prinz, 1997). When an action is performed (e.g. opening of the hand), the motor representation of this action becomes linked to the cognitive representation of any perceptual features this action produces (e.g. seeing an open hand). It follows that the observation of an event that is similar to any perceptual element of a previously encoded sensory-motor association may trigger performance of that action (Brass & Heyes, 2005; Paulus, 2014). Under this model, perception and action are intrinsically linked and the performance of any action (whether in the context of imitation or not) will be guided by the perceptual consequences of that action (Prinz, 1997). This approach predicts that the similarities between previously learned sensory-motor associations will influence the ease of imitation and this has been supported by cognitive studies using stimulus-response compatibility procedures in adults (Brass, Bekkering, & Prinz, 2001; Stürmer, Aschersleben, & Prinz, 2000) and children (Bekkering & Wohlschlager, 2000).

The ideomotor approach largely complements the ASL perspective (Brass & Heyes, 2005; Cook et al., 2014), and Heyes (2013) describes the vertical associations of the ASL approach (see Chapter 3, Figure 3.1) as analogues of the

"dual coding" described by the ideomotor approach. It may be true that the ideomotor approach stresses the role of top-down modulating factors in guiding the links between perception and action (Bekkering & Wohlschlager, 2000; Liepelt, Cramon, & Brass, 2008), however, this has not been considered problematic to the ASL approach (see Heyes, 2013; Cook, Dickinson, & Heyes, 2012; Leighton, Bird, Orsini, & Heyes, 2010; Longo, Kosobud, & Bertenthal, 2008). One discrepancy between these models was highlighted by Brass and Muhle-Karbe (2013) in a recent commentary on the ASL approach, where they state that the association learned in an ideomotor approach is the link between an action and its effect on the environment, while the ASL approach is concerned with links between stimuli and action responses. In their response, Cook et al. (2013), clarify that the ASL model is compatible with this ideomotor perspective and that a focus on links between stimuli and responses is largely due to methodological considerations. The ASL approach predicts that the same links would be developed in the context of actions and their effects. Overall, these two domain-general accounts predict that the correspondence problem can be solved through sensorimotor experience, and predictions of the ASL model explored throughout this thesis will be applicable to an ideomotor approach.

As previously mentioned, automatic imitation has been studied in detail in the context of human cognition yet little work has examined the comparative domain. A comparative perspective is crucial, as the ASL approach predicts that contingent sensorimotor experience, mediated by evolutionarily ancient learning processes, will produce automatic imitation (Heyes, 2005). As predicted by this theory, evidence of automatic imitation has been found in two evolutionary diverse species. Budgerigars (*Melopsittacus undulates)* rewarded for imitating a conspecific perform a foot or beak action learned the associative rule quicker than subjects rewarded for performing an opposite action (Mui, Haselgrove, Pearce, & Heyes, 2008). Similarly, domestic dogs (*Canis lupus familiaris*) rewarded for opening a door with the same body part as their owner (hand/paw or mouth), learned quicker than individuals rewarded for using the opposite body part (Range, Huber, & Heyes, 2011). While these initial results are promising, further study is necessary to examine the full effects of automatic imitation. To date, no study has examined this paradigm in nonhuman primates. Given that evidence of mirror neuron activity at the level of the single-cell is almost exclusively found in studies of monkeys (for a review see Kilner & Lemon, 2013) it is crucial to examine automatic imitation in monkeys to test the assumption that mirror neurons might facilitate imitative behaviour. Automatic imitation is defined within the context of the SRC paradigm, but other behaviours studied by comparative and behavioural scientists are likely governed by the same underlying cognitive processes.

The study of imitation in nonhuman animals has been complicated by conceptual discontinuities and despite efforts to consolidate approaches the field still suffers from a lack of cohesion (Caldwell & Whiten, 2002; Galef, 2013). However, we are interested in motor imitation at the action level, more specifically defined as "the cognitive operations needed to transform visual information into matching motor acts" (p 14; Custance, Whiten, & Fredman, 1999). For example, while rarely considered "true imitation", behaviours previously considered under the heading response facilitation, mimicry, or contagion (see Zentall, 2006) could also be considered "automatic" imitation, potentially mediated by a mirror neuron system. Indeed, according to the ASL approach it should not be surprising to find automatic imitative behaviours throughout the animal kingdom (Heyes, 2011).

Initial attempts to examine imitation in monkeys delivered null results (Mitchell & Anderson, 1993). A classic study of social learning in capuchin monkeys concluded a distinct lack of imitative ability (Visalberghi, 1993). Six capuchins were presented with a transparent, hollow cylinder that containing a food reward. The three monkeys that had not learned to obtain the reward through individual learning were permitted to observe a skilled capuchin manipulate a tool to retrieve the reward. After more than 50 observations each, the unsuccessful capuchins did not learn the task. However, observers

subsequently interacted significantly more often with the apparatus, suggesting exploratory behaviour was socially facilitated, but not socially learned (i.e. possibly stimulus enhancement; see Chapter One for definition). More recent studies of enculturated capuchin monkeys (*Sapajus apella*) suggest similar results with little evidence of motor imitation observed (Fragaszy et al., 2011). However, it could be argued that what is examined in these studies does not specifically tap into the motor imitation that would be facilitated through an ASL approach, instead examining a broader range of social learning mechanisms including affordance learning and goal emulation. Voelkl and Huber (2000, 2007) published two accounts of motor imitation in common marmosets (*Callithrix jacchus*). In an initial study, marmosets were more likely to use the same body part as an observed conspecific (either hand or mouth) to open a box containing a food reward (2000). Additional support was supplied by a subsequent study that analysed details of the marmoset actions. The precise movements of the monkey corresponded with the demonstrator's action only if the individual had previously observed the demonstrator. More recently, using a protocol based on Voelkl and Huber's experiment in 2000, van de Waal and Whiten (2012) discovered that vervet monkeys (*Chlorocebus aethiops*) who observed a conspecific opening a reward-baited canister with their hands were more likely to do the same, whereas those that did not see this behaviour were more likely to use their mouths to open the container. In this present study we hope to examine imitation at this action level in capuchin

monkeys, by looking specifically at automatic imitation. Also, this study will examine predictions based on an ASL approach for the first time with a nonhuman primate species.

Our aims are two-fold. Firstly, using an adapted SRC paradigm, automatic imitation in capuchin monkeys will be examined. Previous studies suggest capuchin monkeys learn primarily from non-imitative forms of social learning but the methodology employed here will permit investigation of more subtle imitative effects in capuchin monkeys. If capuchin monkeys find it easier to learn an imitative rule than a counter imitative rule it would suggest some ability for automatic imitation. Secondly, we hope to examine the generalisability of the ASL approach to a nonhuman primate species. If an ASL approach is accurate, we would predict that any automatic imitative effect will be eliminated, or reduced, through incompatible sensorimotor experience. In a first experiment we address both of these aims. Capuchin monkeys were trained to perform an action upon observing an experimenter perform an action. Half of the monkeys were rewarded for performing the same action, while the other monkeys were rewarded for performing the alternative action. We predicted that if capuchin monkeys automatically imitate motor actions the monkeys that learn the imitative rule should perform better (hypothesis 1). Following this first set of training, the associative rules were reversed; i.e.

55

monkeys that were initially rewarded for imitating were rewarded for performing opposite actions, and vice versa. If capuchin monkeys possess a predisposition to imitate, it might be expected that during this reversal-learning stage those learners that are switching from an incompatible associative rule to a compatible rule should perform better than individuals that experience the alternate reversal. However, if the ASL approach is correct, the experience of learning an incompatible rule should interfere with the prior learning responsible for any initial automatic imitation effect and performance during this reversal-learning stage should be comparable between groups (hypothesis 2). A second experiment further examined the possibility of a predisposition for imitative ability. Two monkeys from experiment 1 were retested on a series of reversal learning sets. Using the same SRC procedure, each monkey learned a compatible and incompatible rule at least twice. If an innate predisposition to imitate exists we predicted that performance on the compatible associative rule will be consistently better than on the incompatible rule (hypothesis 3).

Experiment 1: Methods

Animals and research site

Subjects were eight capuchin monkeys (*Sapajus apella*) from the Living Links to Human Evolution research site at Edinburgh Zoo, housed in mixed species groups with common squirrel monkeys (*Saimiri sciureus*). Capuchins participate

in research sessions voluntarily for additional food rewards (for a comprehensive description of the facility see MacDonald & Whiten, 2011). The monkeys are fed a varying diet of fruit, vegetables, and monkey chow daily. All rewards offered in the course of research sessions were supplementary to their diet. Raisins, sunflower seeds, pineapple juice, and peanuts were used in this study as rewards and to encourage participation. Research was reviewed by zoo keepers at the Living Links research site and ethical approval was granted by the University of Stirling Psychology Ethics committee. All research took place between February 2011 and June 2012.

Materials

Study sessions were conducted in a purpose-built research area that connects capuchin indoor and outdoor enclosures. Capuchins can be temporarily isolated from their group mates in a series of research cubicles consisting of eight cubic compartments (.5m³; see Figure 2.1, a). Capuchins are shut within these cubicles by opaque or transparent slides and each monkey has been trained through positive reinforcement training to feel comfortable during sessions. Capuchins have also been trained to place their hand on the slide door if they want to leave. If monkeys display signs of anxiety or intent to leave the experimenter allows the monkey to exit. Two targets were used in this study. To shape two disparate actions a modified table tennis paddle was used (head

size approx. 15cm diameter with a 10X3cm handle, see Figure 2.2). Alternate

sides were coloured black and white to facilitate colour discrimination training.

A second target was used in the SRC condition that differed in shape and

colour (12x13cm rectangular head with a 10X2 cm handle, see Figure 2.2).

Figure. 2.1: a) Experimental cubicles; b) Presenting target and colour stimulus

to capuchin monkey.

2.1 a)

2.1 b)
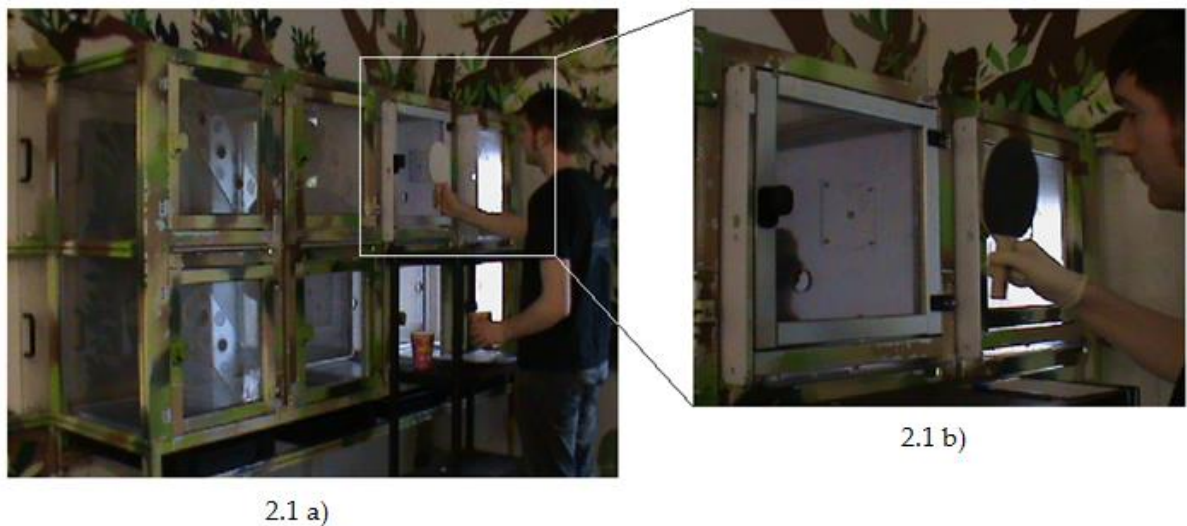
The cubicle window (i.e. the Perspex screen orientated toward the

experimenter) included a small opening in its centre. This opening allowed

juice to be delivered to the capuchin through a mouthpiece connected to a

rubber-tube and syringe.

Figure 2.2: Targets used for training and testing in SRC trials.

On the bottom left side of the cubicle window was a hole (3.5cm diameter) through which food rewards were offered. Sessions were recorded on a Sony Mini DV Digital Video Camera.

Procedure

Shaping behaviours and discrimination learning

The methods employed to shape behaviours was developed during my MSc studies (O' Sullivan, 2011). For monkeys to complete SRC trials, two actions employing disparate body parts were trained: touching the cubicle window with a) their hand and b) their mouth. The training of both actions took place concurrently through positive reinforcement of successive approximations of each action. While the same target was used to cue both actions, a different coloured side was used in each case (i.e. the black side was always presented

when training hand actions and the white side was always presented during the training of mouth actions). To train each individual to touch the cubicle window with their mouth, diluted fruit juice (one part juice to two parts water) was delivered from a syringe to the mouthpiece on the inside of the cubicle. Capuchins learned to bring their mouths to the screen to receive the juice reward. Next, the experimenter presented the training target approx. 5cm in front of the window before the juice was delivered. Once capuchins learned to bring their mouths to the window before the juice was delivered, the juice reward was replaced with a food reward. To train a distinct hand action the training target was presented to the small hole where food rewards were offered. The target was removed once touched by the subject's hand and a food reward was offered. Gradually, the target was moved further from the hole, and the subject, unable to touch the target directly, was rewarded for touching the window with one or two hands. At this point the learned association between stimulus and action was spatial in nature (the mouth action cued by the target presented near the centre of the window; the hand action cued by the target presented nearer the left of the window). Once actions had been learned the target was only presented in the centre of the window, and the capuchin was required to learn a colour association rule (see Figure 2.1 b). Only correct responses were rewarded, i.e. performing an action that corresponded to specific colour. If an incorrect response was performed the experimenter turned his back on the monkey for approximately three seconds, a form of negative

punishment, removing the opportunity to receive further rewards for a set period of time. Once an individual had performed over 85% correct responses on three consecutive research sessions (20 trials per session), the monkey began the SRC trials.

Stimulus Response Compatibility Trials (SRC)

During the piloting of these methods (O' Sullivan, 2011), six monkeys were tested on approximately 300 trials each (mean = 303, SD = 110), and the work reported below expands upon this preliminary work, testing more subjects, and examining considerably more trials. On completion of the colour discrimination trials, individuals were transferred into one of two groups in the SRC condition: a compatible condition or incompatible condition. Based on performance in the colour discrimination stage groups were counterbalanced to include equal numbers of quick discrimination learners; for example, the mean number of research sessions before reaching criterion on the colour discrimination task was 45.75 for subjects in the compatible condition (range = 37-63 sessions) and 45 for subjects in the incompatible condition (range = 31-66). Each session aimed to include 20 individual trials with equal numbers of hand and mouth actions performed, but due to the participatory nature of the research, some sessions included fewer trials. Each SRC session began with four trials testing

baseline action elicitation using the trained colour cue; a series of twenty SRC trials followed, with a further four baseline action elicitation trials after the tenth and twentieth SRC trial. This rewarding of an already learned association was to encourage participation and to assess individual's constant ability to perform both hand and mouth actions discriminately. During an SRC trial a second target (see the target on the right; Fig. 2.2.) was held in front of the experimenter with his left hand and touched with either a) his right hand or b) his mouth. The target was then moved to approx. 5cm in front of the window. Individuals in the compatible condition were rewarded for performing an action with the same body part as the experimenter, while individuals in the incompatible condition were rewarded for using the opposite action. Actions were still performed on the cubicle window. An incorrect response resulted in the experimenter turning his back on the monkey for approximately three seconds. Once a predetermined criterion was reached ($\geq$85% correct responses in three consecutive 20 trial sessions) the reward contingency was to be reversed. However, after 900 trials only one monkey had reached this criterion (Carlos reached the criterion after 500 trials). Because of time constraints, monkeys were switched to the opposite condition regardless of progress after 900 trials. Two monkeys were tested on fewer trials in each condition to examine performance on both associate rules without possible confounding effects of overtraining. These two monkeys completed 320 trials in each condition (Kato and Sylvie). Once reward contingencies were reversed, a

further 500 trials were completed by each monkey (320 in the case of Kato and Sylvie). As monkeys were free to leave in the middle of sessions and each session attempted to test monkeys with 20 trials, monkeys completed on average 10.4 trials more than the established cut-off (900 or 320).

Data Analysis

The monkeys' success on each trial was recorded as a binary response variable (either correct or incorrect). This binary variable was used as the outcome variable in a series of generalised linear mixed models (GLMM) with a binomial distribution and logit link function to test specific hypotheses concerning automatic imitation. As each monkey received multiple trials in each condition, the monkey being tested was included as a random-factor in each model. As performance was expected to improve over trials as monkeys learned the associate rules, trial number in a given block of learning was entered as a predictor variable into each model (the trial number restarted at 1 once associative rules were switched). To test whether monkeys found it easier to learn compatible or incompatible associative rules overall, a model was developed with the associative rule being rewarded entered as a main-effect (i.e. condition). To test hypotheses concerning the ASL hypothesis, a model was developed with an interaction included for condition and order of learning; simple effects of condition were examined when associative rules were first

learned (i.e. order = 1) and when rules are learned for a second time (i.e. order = 2). To describe the contribution of predictor variables to trial success, odds ratios were calculated by back-transforming the log odds ratios. While monkeys completed up to 900 trials in the first block of learning, only the first 500 trials for each monkey were examined (320 in the case of Kato and Sylvie), for two reasons. Firstly, one monkey's associative rule was switched after 500 trials, so a comparison between groups is more valid at this point. Also, to examine any pre-existing bias in automatic imitative ability it is more appropriate to examine earlier performances.

Software

All statistical tests were conducted with the R statistics program (R Core Team, 2014) in the Rstudio environment (RStudio Team, 2014). Models were developed using the lme4 package (Bates, Maechler, Bolker, & Walker, 2015), and graphics were created using the ggplot2 package (Wickham, 2009).

Experiment 1: Results

Descriptive data on overall performance for each monkey, including the number of trials included in the analyses and the proportion of correct responses on each learning block, can be seen in Table 2.1.

Table 2.1: Descriptive data from SRC trials 1-500 for each monkey in both conditions. Mean success on Trials where 1 = successful response and 0 = unsuccessful is included - this measure is the equivalent of the proportion of correct responses in a learning block. Standard error of the mean is included in brackets.

	Rule rewarded in 1st Learning Block	Trials per learning block	Mean Success on Trials (SE)	
			1st Learning Block	2nd Learning Block
Pedra	Incompatible	500	.506 (.022)	.522 (.022)
Figo	Incompatible	500	.500 (.022)	.478 (.022)
Chico	Incompatible	500	.572 (.022)	.444 (.022)
Kato	Incompatible	320	.500 (.028)	.478 (.028)
Total	**Incompatible**	**1820**	**.521 (.012)**	**.481 (.012)**
Carlos	Compatible	500	.658 (.021)	.484 (.022)
Micoe	Compatible	500	.562 (.022)	.502 (.022)
Inti	Compatible	500	.516 (.022)	.478 (.022)
Sylvie	Compatible	320	.512 (.027)	.500 (.028)
Total	**Compatible**	**1820**	**.567 (.012)**	**.490 (.012)**

No main effect of the associative rule being rewarded (compatible/incompatible) was found (Wald chi-square = 2.41, df = 1, p = .121). The order in which the rules were learned was also examined and a significant main effect was identified (Wald chi-square = 25.279, df = 1, p <.001), with a 21.09% reduction in the odds of success after switching conditions. A marginally significant interaction between associative rule and order of learning was identified (Wald chi-square = 3.32, p = .068). When testing the effect of the associative rule in the first block of discrimination learning it was found that the chance of success was significantly higher when learning a compatible rule (16.78% greater odds of being correct; Wald chi-square = 5.74, df = 1, p = .017; see Fig. 2.3, order = 1), however, in the second block of learning, i.e. after associative rules were switched, the type of associative rule being rewarded did not influence chance of success (Wald chi-square = 0.2257, df = 1, p = .635; see Fig. 2.3; order =2). While the analyses reported here examines the first 500 trials (see rationale above), when all data are included in a model similar results are found. A main effect of condition is still absent (Wald chi-square = 2.2393, df = 1, p = .134), and a main effect of order is still present (Wald chi-square = 19.684, df = 1, p <.001). The effect of condition identified in the first learning block drops below the .05 significance cut-off (Wald chi-square = 3.7498, df = 1, p = .053). This is likely due to an improved performance by the monkeys learning the incompatible rule between trials 500 and 950, and the

absence of Carlos, who exhibited the strongest bias and thus had reached criterion by trial 500.

Figure 2.3: Mean proportion of correct responses in first 500 trials for compatible (red) and incompatible conditions (blue) when associative rules are first learned and when rules are switched (Second Learning Block). Error bars represent standard error of the mean (points and error bars are offset to prevent overlap).
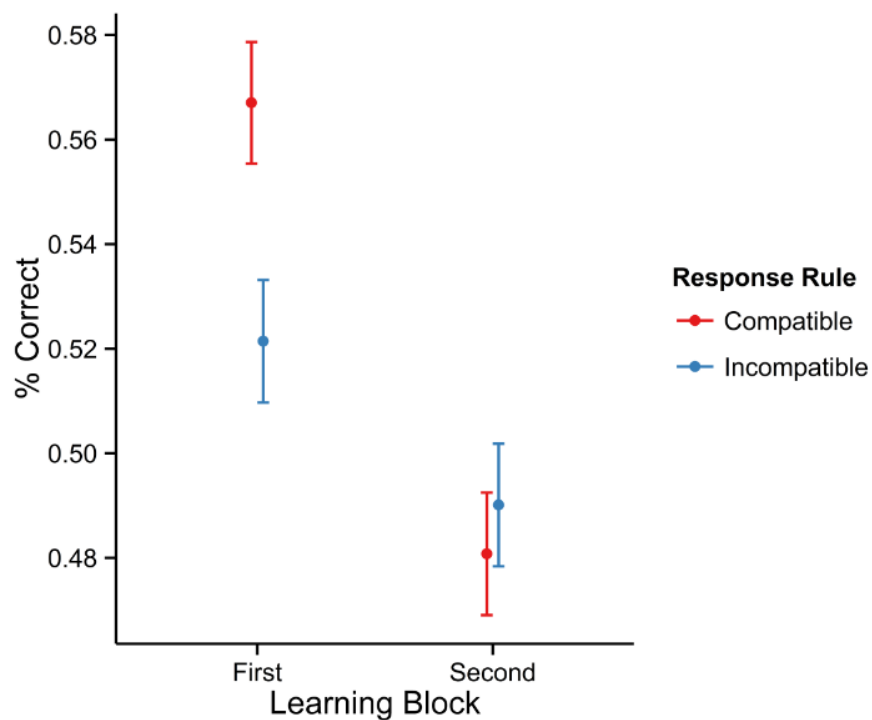
Experiment 2: Methods:

Subjects

This second experiment examined repeated reversal learning of compatible and incompatible rules with two monkeys from experiment 1 (Carlos and Chico). These monkeys were selected as they were the best learners in the initial learning block of their respective conditions (see Table 2.1). These research sessions took place between October 2012 and July 2013, ten months after Carlos' last session in experiment 1, and four months after Chico's last session. Rewards presented and apparatus employed were the same as experiment 1, but slight modifications were made to the procedure.

Procedure

Both monkeys were tested in a similar fashion to experiment 1. Each session began with 4 colour discrimination trials. Once monkeys produced 4 correct responses to the colour stimulus they progressed to action discrimination trials. In the first block of learning Chico was rewarded for performing incompatible responses while Carlos was rewarded for performing compatible actions. Incorrect responses resulted in a three second time-out where the experimenter would turn their back to the monkey. One strategy employed by monkeys in experiment 1 in an effort to maximise rewards was to perform one action repeatedly, therefore receiving half of all rewards in each research session. To

improve speed of learning and to encourage switching between actions correctional procedures were introduced. If monkeys responded incorrectly on a trial the same trial was repeated until the monkey either performed the correct response or an incorrect response was performed a certain number of times. Initially, a trial was repeated up to five times if an incorrect action was performed, however, five consecutive "time-outs" became an overly stringent punishment and subject participation dropped. To increase participation, incorrect responses were instead repeated 3 times (this change occurred after 264 trials for Chico, and after 78 trials for Carlos). These incidences were always scored as a single incorrect trial.

Learning criterion in this second experiment was altered with the intention of decreasing the time taken for monkeys to demonstrate learning. To qualify as having learned an associative rule monkeys had to progress through the following stages. First, a monkey had to provide 65% or more correct responses on a test session consisting of twenty trials. Once this criterion had been met, on subsequent testing sessions monkeys were only tested on ten trial sets. To demonstrate evidence of learning, monkeys had to perform 80% or more correct responses on two consecutive sessions of ten trials (taking place at different testing sessions; i.e. a minimum of an hour between testing). This two-tier criterion was employed as we wanted to offer monkeys sufficient

experience of the reward contingencies in the earlier stages of learning. However, we noticed in experiment 1 that in later stages of learning, monkeys would sometimes lose interest with the procedure after performing a number of consecutive correct responses (possibly due to satiation). It was predicted that reducing session length to 10 trials during later stages of learning would improve motivation to attend to the procedure and would therefore provide a better measure of learning. Once this criterion was met, the associative rule being rewarded was reversed. Over the course of the experiment, Carlos reached the required criterion for the compatible rule three times and the incompatible rule twice. Chico reached the criterion for both conditions twice. To retain comparable numbers of learning blocks for each monkey, Carlos' first four blocks of learning were analysed.

Data analyses

The first response to each trial was coded as a binary response variable (correct or incorrect) – correct responses to a repeated trial were not counted (see description of correctional procedures above). As it was expected that trial number within each learning block would significantly predict success in each learning block, this measure was included in every model that tested our hypotheses. The overall effect of the associative rule being rewarded (compatible versus incompatible) was examined using a generalised linear

mixed model (GLM) with a binomial distribution and logit link function, with condition and monkey as predictor variables. An interaction between condition and monkey was also examined. To examine whether the order in which the associative rules were first learned had an effect on overall performance, a GLM was created with this factor included as a fixed effect (for Chico the incompatible rule was learned first, for Carlos the compatible rule was learned first). Finally, to examine if there was any change in performance over repeated opportunities to switch between associative rules, the number of the learning block (1st-4th) was included in a GLM as a predictor variable. These analyses were also performed for Chico and Carlos separately and the same results were identified so only analyses with individual included as a fixed factor are reported. Analyses were performed with the same software packages as reported in experiment 1.

Experiment 2: Results

Descriptive data for the number of trials it took before each monkey reached the learning criteria can be seen in Table 2.2. A GLM identified trial number within a learning block as a significant predictor of success (Wald chi-square = 71.501, df = 1, p <.0001), with an increase of .27% in the odds of success as trial number increases by 1 in a learning block. No overall main-effect of condition was identified (Wald chi-square = 1.707, df = 1, p = .191; see Figure 2.4a).

Table 2.2. Number of sessions before each monkey reached learning criteria for each learning block. The initial of the rule learned is in brackets after the trial number (compatible =c; incompatible =i).

No. Trials Before Reaching Criterion

Learning Block	Carlos	Chico	**Total**
1	200 (c)	204 (i)	**404**
2	166 (i)	267 (c)	**433**
3	60 (c)	551 (i)	**611**
4	280 (i)	541 (c)	**821**
5	235(c)		
Total	**941**	**1563**	**2269**

A significant effect of monkey was found with Carlos performing better on average (65.36% greater probability of being correct; Wald chi-square = 25.161, df = 1, p<.0001), and a significant interaction was found between monkey and condition (Wald chi-square = 9.443, df = 1, p = .0021). There was no difference between conditions for Chico (Wald chi-square = .343, df = 1, p = .558) while Carlos performed significantly better on compatible trials (59.32% greater chance of a correct response; Wald chi-square = 10.806, df =1, p = .001).

Figure 2.4: a) Mean proportion of correct responses in experiment 2 when differentiated by a) the associative rule being rewarded (compatible or incompatible); and b) the first associative rule that each monkey was rewarded for in both experiment 1 and experiment 2. Error bars represent standard error of the mean.
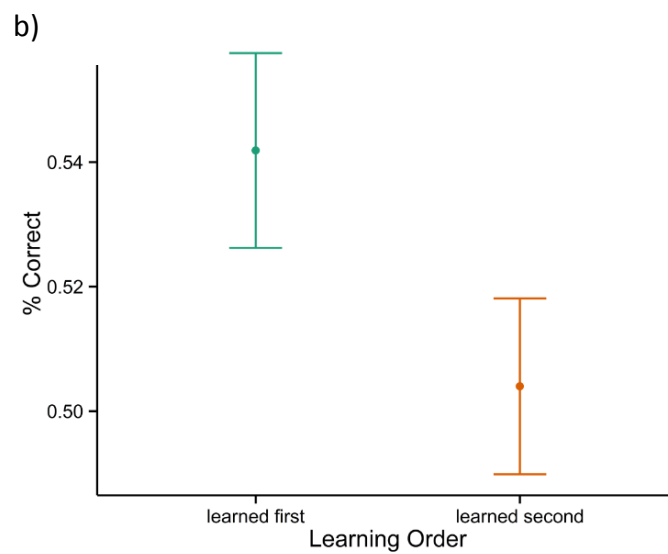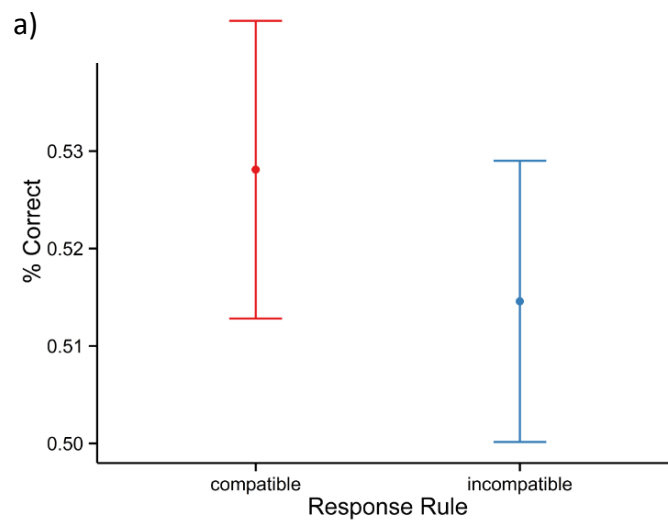
In a separate GLM, the effect of whether learning a rule first influenced success identified a main effect of learning a rule (Wald chi-square = 5.235, df = 1, p = .0221; see Figure 2.4b). However, an interaction between monkey and learning order was found (Wald chi-square = 5.915, df = 1, p = .0150), and when simple effects are examined the effect of learning order is only significant for Carlos (Wald chi-square = 10.806, df = 1, p = .0010), not for Chico (Wald-chi-square = .0343. df = 1, p = .558) suggesting the main effect is driven by Carlos' performance.

Finally, modelling whether learning block has a significant effect on success identified a main effect of learning block (Wald chi-square = 51.006, df = 1, p<.0001, see Figure 2.5), where success was reduced on average by 25.77% for each successive learning block; there was also a significant interaction between monkey and learning block (Wald chi-square = 4.817, df =1, p = .0282), where the effect of learning block was significantly greater for Chico (Wald chi-square = 46.419, df = 1, p <.0001; odds ratio = -31.56%) than Carlos (Wald chi-squared = 10.836, df = 1, p = .0010; odds ratio = -18.14%).

Figure 2.5: Mean proportion of correct responses by learning block with standard errors represented by error bars.
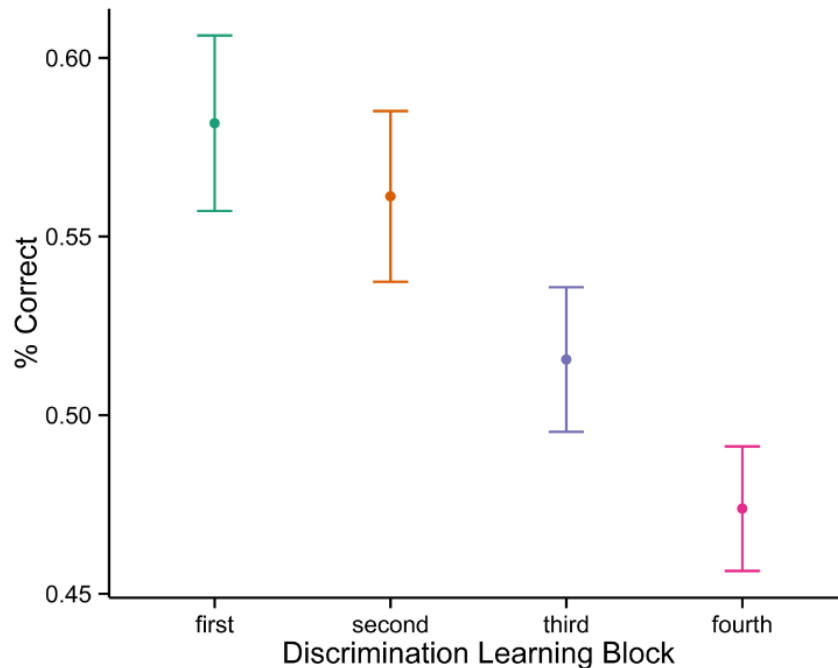
Discussion

The first time monkeys had to learn an associative rule between observing an action stimulus and performing an action, the individuals who learned a compatible rule performed significantly better than those who were required to learn an incompatible association. This finding is the first evidence of automatic imitation in a nonhuman primate, contributing to existing comparative evidence in birds, and dogs (Mui et al., 2008; Range et al., 2011). Similarly, while evidence of action imitation in monkeys is scarce (i.e. Fragaszy, Deputte, Cooper, Colbert-White, & Hémery, 2011), this result complements evidence of

body part matching (mouth and hand) previously found in other New World species (Voelkl & Huber, 2000, 2007b) and more recently in Old World monkeys (van de Waal & Whiten, 2012). This is the first evidence of automatic imitation in capuchin monkeys, but it is worth noting that while monkeys performed better in initial trials with imitative rules, only one monkey reaching the pre-set criterion level that would have demonstrated more valid evidence of having learned the discrimination rule. The difficulty that monkeys faced in transferring their previously learned colour-action association skills to an action-action associative paradigm demonstrates that automatic imitation is not necessarily "automatic" in the sense of being reflexive and effortless or that action matching is readily available to capuchin monkeys (as evidenced by previous research; e.g. Fragaszy et al., 2011). Instead, the effect identified here may be a more implicit bias that this specific procedure can tap into. If an innate action-matching system is present in capuchin monkeys, as is supposed in humans and other nonhuman primates (Ferrari et al., 2006; Meltzoff & Moore, 1997), it is certainly not overtly evident.

To examine the origin of imitative ability, predictions were made concerning imitative learning that followed counter-imitative learning. The better performance of imitators in the first learning block did not persist once reward contingencies were reversed. The AIM hypothesis predicts that imitation is

facilitated by proprioceptive feedback loops where a performed action can be compared to an observed action in a supramodal representational system (Meltzoff & Moore, 1997). This system would underlie imitative action regardless of previous experience. Here it was found that the experience of responding to an observed action with a different action in the initial block of learning eliminated any bias toward imitation in the second block. If an innate supramodal system facilitates action matching it might be expected that a bias to imitate would persist following incompatible training. However, it is important to note that this null finding cannot be interpreted as direct evidence against an AIM approach. A multimodal action matching system that exists at birth does not discount later learning that may override an innate bias. It is also worth noting that while the associative rule being rewarded in the initial block significantly predicted performance (which was not the case in the second block of learning), the interaction between order and condition was only marginally significant and so this difference in performance between the first and second learning block is tentative. Nevertheless, the comparable level of success observed in both conditions in the second block of learning corresponds with predictions made by the ASL account of imitation and effects observed in humans and other animals (Catmur et al., 2007; Mui et al., 2008; Range et al., 2011). In a second experiment, further efforts to examine imitative ability in two capuchin monkeys showed no evidence that imitation is intrinsically easier than counter-imitation overall. One monkey did perform better when

77

compatible trials were rewarded, and this might be interpreted as a bias to imitate. However, without discovering a similar effect in the monkey initially rewarded for performing incompatible responses, it is difficult to conclusively state whether this finding is driven by a bias towards imitation, or towards the first-learned association. Together, these studies provide support for an associative explanation of imitation. Importantly, these results are also compatible with other accounts of imitations that stress the role of sensorimotor experience (i.e. the ideomotor approach), and indeed some proponents of these alternative accounts have stated that associative learning is likely the mechanism that binds dual codes (Paulus, 2014). However, support for an associative account rests on a lack of evidence for a disposition to imitate action, and due to the small sample studied here (especially in experiment 2) it may be that the design had insufficient statistical power to detect a smaller effect.

Nonetheless, these results contribute to a growing body of evidence in support of the ASL approach to imitation in human and nonhuman animals (Catmur et al., 2008, 2009; Mui et al., 2008; Range et al., 2011). The best evidence in support of an innate action matching system comes from the literature on neonatal imitation in human and nonhuman primates (Ferrari et al., 2006; Meltzoff & Moore, 1977), but the reliability of such results has been questioned on

numerous occasions (Anisfeld, 1996; Hayes & Watson, 1981; Lodder et al., 2014; Ray & Heyes, 2011a). While a recent review has suggested that null findings may be the result of low statistical power (Simpson et al., 2014), the debate over the validity of a neonatal imitation effect is not yet resolved. Also, there are still many questions to be answered concerning imitation in infancy. For example, while numerous studies have reported evidence of neonatal imitation in primates (Ferrari et al., 2006; Meltzoff & Moore, 1983), it is unclear why this tendency diminishes after a number of weeks (e.g. Ferrari et al., 2006) to emerge again around 2 years of age (Dickerson, Gerhardstein, Zack, & Barr, 2008). More theory-driven research is necessary to test hypotheses related to the ontogeny of imitative ability and its underling neurological basis. Some recent studies of imitation in infants and children have found support for associative accounts (de Klerk et al., 2014; Paulus, Hunnius, Van Elk, & Bekkering, 2012), and in the next chapter I too will test predictions based on the ASL approach in human children.

While examples of imitative learning are rare in capuchin monkeys, the role of imitation in facilitating affiliation are also worth considering here. The automatic imitation effect identified in this study complements evidence that capuchins are able to recognise corresponding actions of others, for example, when being imitated (Paukner, Suomi, Visalberghi, & Ferrari, 2009). However,

if the mechanism that links observable action to an executed action is forged through associative learning then it is possible that monkeys that have been trained to respond in counter-imitative ways may show increased interest and affiliation towards those that perform contingent non-matching actions. The affiliative facet of imitation needs to be further examined in the light of these findings. For example, if it is discovered that imitation's role in affiliation is robust to manipulation (i.e. to incompatible training) then the proposal that imitation is learned should be re-evaluated.

Previous research of reversal learning has discovered a robust effect whereby if reward contingencies are reversed after an associative rule is learned, the learning of the new rule generally takes longer than the initial learning (Feldman & Albuquerque, 1968). This effect was observed in experiment 2. However, in successive reversals it is generally found that learning is quicker and fewer mistakes are performed (Bond, Kamil, & Balda, 2007; Feldman & Albuquerque, 1968). Due to these previous observations it was expected that alternating between associative rules would eventually become easier for our two subjects in experiment two. This was not the case, with one monkey taking longer to reach criterion after each consecutive reversal (Chico; see Table 2.2). Adoption of "win-stay, lose-shift" strategies in these types of paradigms are thought to be indicative of cognitive flexibility and have been noted in apes (for

a review see Shettleworth, 1998), and corvids (Bond et al., 2007). Here, we found no evidence of flexible learning strategies, which corresponds with findings from previous reversal learning experiments in capuchins (Beran et al., 2008). However, the task examined here is more complex than the tasks generally used in tests of reversal learning. Rather than making a choice between two available stimuli (e.g. Bond et al., 2007), monkeys had to perform two distinct actions towards two distinct stimuli, in effect learning two associations instead of one. This increased level of complexity may make comparative assessment of learning ability in capuchin monkeys problematic.

Overall, this study contributes to a growing literature in support of the ASL approach to imitation. However, this is only a first step towards understanding the ontogeny of this ability in primates. Further work incorporating the SRC paradigm with New World and Old World monkeys is necessary to provide robust evidence of automatic imitation in nonhuman primates. It has been suggested that automatic imitation can become a tool through which we can examine the behavioural artefact of mirror neurons (Heyes, 2011). If that is to be the case, and if the study of automatic imitation effect is to become an important tool for answering questions of social cognition, the answers will be found in future, careful and controlled cognitive and neuroscience experiments.

Chapter 3: Automatic imitation in children

Due to the correspondence problem, copying the behavioural morphology of an action is often considered to be cognitively demanding (Nehaniv & Dautenhahn, 2002; discussed in detail in Chapter One). Imitating actions that in some cases are opaque to the imitator requires a mechanism for transforming sensory information into a corresponding matching action. In the preceding chapters, two opposing models explaining how this correspondence problem is solved were examined; one approach predicts humans are born with an inter-modal representation space where proprioceptive feedback from an action can be compared to a sensory representation of the same action, facilitating action imitation (the active inter-modal mapping hypothesis, AIM; Meltzoff & Moore, 1997). On the other hand, domain-general accounts proposes associative learning links sensory and motor representations to overcome the correspondence problem (ASL, and ideomotor approach; Heyes & Ray, 2000; Brass & Heyes, 2005). In Chapter Two, predictions of these accounts were examined in capuchin monkeys providing support for a domain-general model of imitation, focussing on the ASL model. The ASL approach has also been extensively studied in adults, however, no study has yet tested its predictions in children. In this chapter I will discuss research on the development of imitative ability in humans and further test predictions of an associative account.

There is no consensus in the field of developmental psychology about when infants first exhibit a capacity for imitation. However, researchers predominantly fall into one of two camps. Some believe an imitative faculty is present from birth (Meltzoff & Moore, 1997; Nagy et al., 2005; Simpson, Murray, Paukner, & Ferrari, 2014), while others believe imitative ability develops throughout the first years of life (Jones, 2009; Ray & Heyes, 2011). The observation that within hours of being born infants imitate facial gestures was first reported by Meltzoff and Moore (1977) and there have been many attempts to replicate these findings, with mixed results. Some studies report evidence of a number of actions being imitated from birth including tongue protrusion, mouth opening, finger movement, and emotional expressions (Field, Woodson, Greenberg, & Cohen, 1982; Meltzoff & Moore, 1977, 1983; Nagy et al., 2005; Nagy, Pilling, Orvos, & Molnar, 2013), while others find either selective imitation of only certain actions or no imitation at all (Anisfeld et al., 2001; Hayes & Watson, 1981; Heimann, Nelson, & Schaller, 1989). Recent studies in nonhuman primates have identified further evidence of neonatal imitation of mouth opening and tongue protrusion in chimpanzees (*Pan troglodytes*, Bard, 2007; Myowa-Yamakoshi, Tomonaga, Tanaka, & Matsuzawa, 2004), and evidence of lip-smacking and tongue protrusion imitation in 3-day old rhesus macaques (*Macaca mulatta*, Ferrari et al., 2006; however, there was no evidence of neonatal imitation of these actions when infants were 1, 7 or 14 days old, and no evidence was found of mouth opening or hand opening imitation). Evidence

from nonhuman primates lends weight to the notion of an evolved and innate action matching system that is at least sensitive to certain actions.

However, reviews of the evidence often draw conflicting conclusions about the presence of such a system. In the same year that Meltzoff (1996) described the human infant as an imitative generalist, Anisfield (1996) declared that only tongue protrusion is imitated by neonates. More recent reviews of the literature have been similarly inconsistent (Lodder et al., 2014; Ray & Heyes, 2011a; Simpson et al., 2014). Ray and Heyes (2011) compare the number of positive and negative results for the main gestures studied and conclude that while reliable evidence of tongue protrusion is available, there is no support for the other gestures. Evidence of imitation of tongue protrusion has been explained as an innate reflex possibly related to feeding (Jacobson, 1979) or an artefact of general arousal (Jones, 1996). The notion that tongue protrusion may be an innate response to certain arousing stimuli that may facilitate exploration is supported by an increase in tongue protrusion in response to music (Jones, 2006), lights (Jones, 1996), and moving objects (Jacobson & Kagan, 1969). However, a recent study found that imitated tongue protrusion was not related to an increase in hand or finger movement or general activity state which suggests no link between tongue protrusion and general arousal (Nagy et al., 2013). Whether through imitation or through arousal, the tongue protrusion

effect is reliable, but the ability to imitate one action is not convincing evidence of a generalised multi-modal imitation mechanism (Ray & Heyes, 2011). In fact, some have argued that the "tongue protrusion effect" may lead to evidence of other actions being imitated. Anisfeld (1996) argues that the scoring methods used in some studies could generate false positive findings of other imitative actions as a by-product of a tongue protrusion effect. For example, the second most widely studied action in this literature is "mouth opening". Evidence of mouth opening imitation is often based upon a comparison of the frequency of mouth opening actions performed by an infant when tongue protrusion is being modelled by the experimenter and when mouth opening is being modelled by the experimenter. If an infant performs more mouth opening actions while the same action is being modelled, evidence of neonatal imitation is reported. However, higher rates of mouth opening when that action is being modelled may be an artefact of tongue protrusion imitation limiting the potential for mouth opening actions during the modelling of tongue protrusion. The frequency of multiple actions within a given response period are not mutually exclusive and this is not taken into account in many studies.

Other reviews draw more confident conclusions concerning the validity of neonatal imitation. A recent example of such a review drew attention to discrepancies between sample sizes reported in studies that have found a

neonatal imitation effect and those that have not (Simpson et al., 2014). The authors examined the effect sizes reported in publications that observed effects of neonatal imitation and calculate that a sample size of 26 is necessary to find the smallest effect size reported in the literature (with a given power of 80%; Cohen, 1988). The authors subsequently show that most studies with the required sample size find evidence of neonatal imitation while those that do not meet the requirement find null results. While the authors are correct to draw attention to the importance of a priori power analyses they fail to take into consideration criticisms of coding discrepancies highlighted by previous reviews (Anisfeld, 1996). Furthermore, Simpson and colleagues (2014) report that the effect sizes found in studies of neonatal imitation range from small to large (see Cohen, 1992), yet use "the most conservative estimate of effect size" in their power analysis (p. 7). This power analysis then provides the sample size required to find the smallest effect reported in the literature, not the "real" effect of neonatal imitation which is likely larger. An analysis with a less conservative estimate of effect size would recommend a lower sample size and the authors' critique would need to be revaluated.

Further work is necessary to confirm the presence of a neonatal effect. Systematic reviews of the subject use different criteria on which to base conclusions (e.g. Nagy et al., 2013; Ray & Heyes, 2011; Simpson et al., 2014), and

while a meta-analysis of existing data would be useful, it is also important that further empirical work examines this effect with criticisms of methods, coding practices, and data analyses taken into account. While a consensus answer to the neonatal imitation question is not forthcoming some have suggested that overconfidence in neonatal imitation may distract from the empirical study of how imitative ability develops throughout infancy (Jones, 2007). Regardless of the presence or absence of innate imitative ability it is important to consider both predispositions to imitation and also the influence of ontogenetic processes.

What is the alternative to the innate imitation system proposed by Meltzoff and Moore (1997)? First of all, it is worth noting that an ability to imitate at birth does not preclude the involvement of learning processes later in development. In fact, some argue that evidence of imitative ability diminishing over the first few months (Ferrari et al., 2006; Fontaine, 1984) suggests that neonatal imitation may be a specific adaptation for early bonding and a different imitation faculty develops later to facilitate learning (Oostenbroek, Slaughter, Nielsen, & Suddendorf, 2013). There are few studies of the development of imitation in infancy, a deficiency that Jones (2007) attributes to the widely held belief that infants imitate from birth, however, early work in the field of development psychology suggested imitation developed gradually through stages. Before

Metlzoff and Moore's seminal work on neonatal imitation, Jean Piaget (1951/1962) proposed a stage model of imitation that did not presuppose any innate imitative ability. By studying his own children Piaget described the development of imitation throughout the first two years. Observations of infants less than a week old that cried upon hearing another infant cry (see Chapter 5 for further discussion of emotional contagion), and imitation of head movements at three months were not attributed to intentional imitation (the latter effect was described as an effort on the part of the infant to maintain the perceptual experience of movement). However, after six months, all of Piaget's children imitated actions already present in their repertoires and which they could see themselves perform. Subsequently, Piaget noted that imitation of actions unobservable to the infant seemed to develop through practice. Actions that produced sounds were imitated sooner, possibly due to sounds acting as indices allowing the mapping of an observed action performed by another onto the unobservable action performed by the infant (Piaget, 1951/1962; this observation corresponds with the ASL model's predictions that certain stimuli will facilitate the link between motor and sensory representations of opaque actions; see Figure 3.1).

Before performing novel actions, Piaget described how his children made approximate attempts at imitating these actions. For example, upon seeing an

adult make a pointing gesture, one of Piaget's children would attempt various finger movements, but did not imitate the specific pointing action until later. At these later stages of development, actions were only imitated when they were in some way analogous to actions already in the infant's repertoire, and responses were often only approximate as children would try out actions to "see whether one of them will fit the model" (Piaget 1951/1962l p . 51). In the second year, Piaget observed these imitative attempts to become more exact but often retained some level of gradual approximation, or training, before expert imitation was achieved. Finally, in the middle of the second year, more advanced imitative ability was noted, and Piaget describes that the experimentation observed in the earlier stages becomes internalised facilitating quicker imitation of novel actions. While the generalisability of these findings is limited by the preliminary nature of these case studies, this work is still the most detailed longitudinal account of the development of imitative ability in infancy, and suggests that the imitative faculty develops gradually throughout infancy. However, some more recent work has furthered our understanding of the development of early imitative ability.

More recent observations align quite closely with Piaget's earlier reports. Jones (2007) conducted a cross-sectional study of imitative behaviour in 162 infants from 6 months of age to 20 months. Eight actions were modelled by a parent

and were categorised according to certain properties, including whether the actions were visible when being performed, or whether the actions produced a sound. Reliable imitation of any kind was not identified at 6 months, and actions that produced sounds were first imitated between 8 and 12 months of age. The final actions to be imitated were silent and were not observable by the infant performing them. Interestingly, one of these actions was tongue protrusion which was not imitated reliably until 16 months. These results closely match an earlier case-study performed by the same author (Jones, 2006). Other studies support the idea of imitative ability developing throughout the 2nd year. Nielsen and Dissanayake (2004) found that infants start imitating synchronous actions around 18 months of age. Masur and Rodemaker (1999) found that at 1 year of age infants are already imitating actions performed on objects, but that intransitive actions only begin to be imitated consistently at around 17 months. These findings describe a different picture of imitation in infants and how it may develop throughout infancy. Regardless of whether imitation is innate or learned it is clear that imitation in the first years of life is limited in its diversity. However, by the age of three it is widely recognised that children are highly competent imitators, often over-imitating unnecessary actions to achieve outcomes (Horner & Whiten, 2005; McGuigan, Whiten, Flynn, & Horner, 2007; Piaget, 1951/1962). If imitation develops throughout infancy, it is necessary to explain what shape this learning may take.

An associative account of imitative ability was outlined in the first two chapters. Here, this model will be summarised briefly with a focus on its predictions in relation to the development of imitation in humans. The Associative Sequence Learning (ASL) approach was developed by Ray and Heyes in 2000 to describe the cognitive process facilitating imitative learning. This model has subsequently been adapted to describe the development of mirror neurons (Catmur, Walsh, & Heyes, 2009; Heyes, 2010). The ASL theory proposes that an imitator develops links between sensory and motor representations of actions through experience. Vertical associations are created between sensory and motor representations of actions through experience (see vertical lines between sensory 1 and motor 1 in Figure 3.1). This experience occurs whenever sensory and motor representations are available at the same time. For example, this includes occasions where someone performs an action they can see, when observing an action in a mirror, and during synchronous social interactions (Heyes & Ray, 2000). These sensory-motor associations are created prior to imitation, and facilitate imitation when an action is observed at a later time. Other stimuli may facilitate the link between sensory and motor action units (see stimuli 1, 2, etc. in Figure 3.1). For example, the vocalised word "smile" may become associated with both the performance of a smile and the observation of someone else smiling, facilitating an indirect association between sensory and motor representations of an action. This indirect route to

91

forming an association is thought to be especially important when an action is opaque.

Figure 3.1. The Associative Sequence Learning approach redrawn from Heyes and Ray (2000).
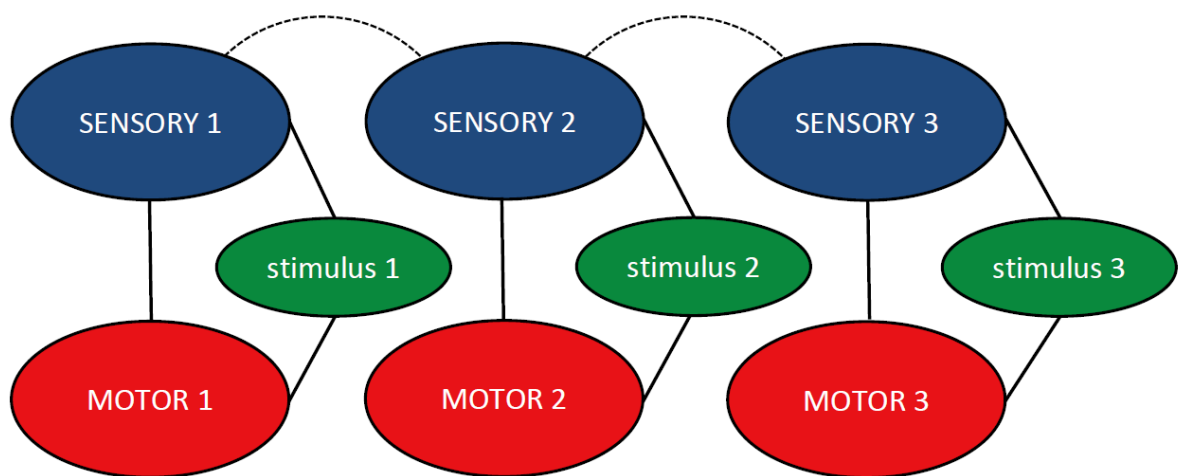
The horizontal lines presented in Figure 3.1 represent associations between sensory representations of action units that allow more complex behavioural strings to be executed. Heyes and Ray (2000) suggest that these horizontal associations can be mediated by contextual cues (i.e. the completion of an earlier action). As previously mentioned, this approach is closely aligned with the ideomotor approach discussed in Chapter 2 which makes similar predictions concerning the influence of experience on imitative ability. The ASL approach has been applied to explain mirror neurons where sensory and motor

representations are instead discussed as sensory and motor neurons (Heyes, 2010). Connections between neurons develop through sensorimotor experience and after an association has been created a motor neuron may fire solely upon seeing an action being performed. This model is gathering empirical support from studies of adult humans through the analyses of automatic imitation effects.

Automatic imitation is not another discrete category of social learning to be included with the already defined mechanisms (see Chapter One; or Hoppitt & Laland, 2008). Instead, automatic imitation is a stimulus-response compatibility effect that is detected when the presentation of an action stimulus (e.g. a picture of a hand opening) facilitates the performance of that action and interferes with the execution of an opposite action (e.g. closing a hand; for a review see Heyes, 2011). This automatic imitation effect may be a behavioural indicator of the vertical associations between sensory and motor representations of an action (or mirror neuron activity), and the effect has been reliably identified in numerous studies (e.g. Brass, Bekkering, Wohlschläger, & Prinz, 2000; Heyes, Bird, Johnson, & Haggard, 2005; Stürmer, Aschersleben, & Prinz, 2000). More recently, automatic imitation has been employed to test assumptions of the ASL hypothesis (Heyes, Bird, Johnson, & Haggard, 2005; Press, Gillmeister, & Heyes, 2007). For example, in a first experiment Heyes and colleagues (2005)

found that when participants were asked to open or close their hand after seeing a picture of a hand begin to move they were quicker when the stimulus hand was performing a compatible action and slower when it was performing an incompatible action. In a second experiment participants were trained to respond to seeing an open hand by closing their hand, and to open their hand after seeing a closed hand (incompatible sensorimotor experience). A day later, participants were asked to perform the same simple reaction task that produced an automatic imitation effect in the first experiment; however, after the incompatible sensorimotor training the automatic imitation effect was eliminated. This suggests that automatic imitation is reliant on experience and can be disrupted by counter-imitative training. A more recent study examined a similar effect in mirror neuron activity (Catmur et al., 2008). Some participants were given counter-imitative training where they were required to move their foot after seeing a hand move and move their hand after seeing a foot move; other participants were given compatible imitative training. Twenty-four hours later participants' brains were scanned in a functional magnetic resonance imager while being presented with video stimuli of hands and feet moving. Activity in brain areas associated with mirror neuron function was observed in both groups of participants, however, areas of the mirror neuron system that were active upon seeing hand actions in the group that had received compatible training were active when observing foot actions in the incompatible group; the opposite effect was observed when stimuli were

reversed. This suggests that experience of contiguous sensory-motor activity forges connections between representations of actions that can be observed at the neurological level, even if the sensory and motor actions are different. Support for the ASL model is growing based on experimental evidence with adults, however, for the model to be useful it must take into account the real sensorimotor experience of infants and children, and explain whether this experience can facilitate the development of imitation.

A crucial aspect of the ASL approach to imitation is that experience forges connections between sensory and motor representations of an action, and while this has been explored in laboratory settings through training protocols (Gillmeister, Catmur, Liepelt, Brass, & Heyes, 2008; Heyes et al., 2005) it is less clear whether this type of experience is common in an infant's environment. A few studies have examined imitation of both parents and infants in naturalistic play settings. Pawlby (1977) observed mother-infant interactions between the ages of four and eight months and found that approximately 16% of interactions involved some form of imitation by the mother. Kokkinaki and Vitalaki (2013) found that three-four imitative interactions (including both actions and vocalisations) took place every ten minutes between mothers and infants, and grandmothers and infants when children are 2 to 10 months, with 66%-79% of imitative interactions performed by the caregiver. Similarly, one

study found that parents imitate a child's vocalisation once every 4-5 minutes (Kokkinaki & Kugiumutzakis, 2000), and an earlier study found that 41% - 57% of non-cry vocalisations were matched between infants and mothers, primarily driven by mothers imitating infants (Papousek & Papouskek, 1989). It is worth mentioning that in many of these studies of free-play, infants are also found to imitate which suggests early imitative ability (e.g. Kokkinaki & Kugiumutzakis, 2000; Theano Kokkinaki & Vitalaki, 2013). Flynn, Masur, and Eichorst (2004) examined factors that predict imitation between mother-infant dyads and found that the rate of imitation by a mother was predicted by the imitative opportunities available to the mother (i.e. as infants performed more actions or vocalisations imitation opportunities increased). On the other hand, an infant's imitation of a mother's action was better predicted by the infant's own motivation to perform actions independently, and was not related to opportunities that afforded imitation. This suggests that imitation of actions is primarily driven by parents imitating infants, and that infant imitation is more likely to be the result of chance. Together, this research suggests that appropriate sensorimotor experience takes place during an infant's development, however, some authors question whether the amount of experience observed in free-play scenarios would be adequate to develop imitative ability (Simpson et al., 2014). Nevertheless, sensorimotor experience does occur during infancy so the next step is to observe the effect of this interaction on behaviour. Building upon evidence of synchronous and imitative

experience in infancy and childhood, here we set out to test the effect of this influence on behaviour.

In the current study I aimed to test specific predictions of the ASL approach to imitation in children. Taking inspiration from previous studies of automatic imitation in adults and animals (Range et al., 2011; Stürmer et al., 2000) a method for assessing automatic imitation in children was developed. While all evidence suggests that ability to imitate actions is established by the age of three (Jones, 2006; 2007; Horner & Whiten, 2005; Masur and Rodemaker, 1999; Piaget 1951/1962), to begin to examine the ASL approach children between the ages of three and seven were tested. The decision to study children already possessing imitative ability was largely due to a methodological limitation, as a previous study has found that young children (three-four) struggle with the task that we employed (see pilot study reported in Simpson & Riggs, 2011). This task required participants to make one of two actions in response to an action performed by an experimenter. Four different actions were used: hand clapping, hand waving, hand closing, and pointing. One game required participants to clap or wave, the other game required participants to close their hands or point. In compatible conditions participants were asked to respond with the same action as the experimenter; in incompatible conditions children were asked to perform the opposite action. Each participant experienced all

iterations of the game. We expected strong stimulus-response compatibility effects as suggested by previous research on automatic imitation (Brass et al., 2001; Stürmer et al., 2000), however, the primary aim of our study was to predict specific automatic imitation effects based on the ASL hypothesis.

The action sets used in this study were chosen based on two criteria. First, all actions had to be simple to perform. Secondly, it was expected that children have a greater amount of sensorimotor experience performing and observing two of the actions. To my knowledge no previous study has described the occurrence of specific synchronised actions in childhood and therefore these actions were chosen through discussions of synchronous actions that children regularly perform during games and social interactions. It is thought that both clapping and waving are performed in synchrony during some social interaction (e.g. applause and waving goodbye), and are also performed together during some games. On the other hand, pointing and hand closing, while equally easy to perform, were not considered to be performed in synchrony or to be imitated as often. Our first prediction based on the ASL approach of imitation is that automatic imitation effects (i.e. the difference in reaction time between imitating actions and performing different actions) will be greater for actions that have been imitated more in past interactions (the commonly imitated action set). Also, the ASL approach predicts that external

stimuli may facilitate the association of visual and motor properties of an action. Knowing that reactions times are faster when responding to multisensory stimuli (Andreassi & Greco, 1975; Hershenson, 1962) we may then predict that an automatic imitation effect may be stronger for an action that produces other environmental stimuli. The only action that produces a non-visual stimulus is clapping which also produces sound. We predict that the automatic imitation effect will be greatest for this action. Finally, we predict that if automatic imitation develops through experience that short periods of counter-imitation experience preceding imitation trials may reduce reaction times when imitating. If this is the case we should find that when incompatible experimental trials precede imitative trials that automatic imitation effects will be suppressed. It is difficult to predict whether, or how, age might affect automatic imitation. For example, it might be expected that cumulative sensorimotor experience throughout development might facilitate quicker reaction time on imitative trials in older children while making it more difficult to inhibit imitative responses during counter imitative-trials; this might lead to an increase in automatic imitation through development. However, children get better at inhibiting imitative responses as they get older (Simpson & Riggs, 2011), which may lead to quicker reaction times when counter-imitating, subsequently reducing automatic imitation effects in older children. These developmental effects together may cancel themselves out leading to a stable automatic imitation effect throughout development with overall quicker

reaction times for both imitative and counter-imitative responses. Due to the uncertainty over the direction of these effects, age related variation will be examined without a priori hypotheses.

Methods

Participants

Participants were 101 children aged between 3 and 7. Twenty-nine participants were excluded from the analyses for either not finishing the research session, for not performing more than 60% correct responses in any one of the four conditions, for not paying attention to the experimenter during the stimulus presentation, or for having parents or guardians interfere in their responses (mean age of excluded participants = 4.33 years, standard deviation, SD = 1.24 years). Seventy-two participants were included in the analysis; mean age was 5.74 years (SD = 1.29 years) and 39 participants were female. Participants were recruited at the Royal Zoological Society of Scotland's Edinburgh Zoo in July 2013, and voluntarily completed research sessions for rewards of stickers. Ethical approval was granted by the University of Stirling Psychology ethics committee, and consent was given by the child's parent or guardian before the session began.

Materials

A Sony CX405 Handycam was used to record each research session.

Design

Over the course of a research session four different games were played using two different sets of action. For two of the games participants had to produce actions that are commonly imitated or are commonly performed during synchronous activity (Commonly Imitated Set, CIS). The actions chosen for the CIS were "waving" and "clapping" (see Figure 3.2, a-b), as children often clap hands together in games and during applause, and waving is also often imitated or performed in synchrony (e.g. in waving goodbye). Furthermore, waving and clapping have been identified as two of the earliest actions to be imitated by children (Jones, 2007). The actions performed in the other action set (the Rarely Imitated Set, RIS) were "pointing" and "hand closing" (see Figure 3.2, c-d). While these behaviours are as easy to perform as the CIS there is no evidence that they are performed in synchrony to the same degree. Using a stimulus-response compatibility paradigm two different games were played with each action set; both games required the participant to respond to the actions performed by the experimenter.

Figure 3.2. Action stimuli used in study; arrows indicate movement. Actions A (clapping) and B (waving) are part of the commonly imitated set of actions while actions C (hand closing) and D (point) are considered rarely imitated actions.
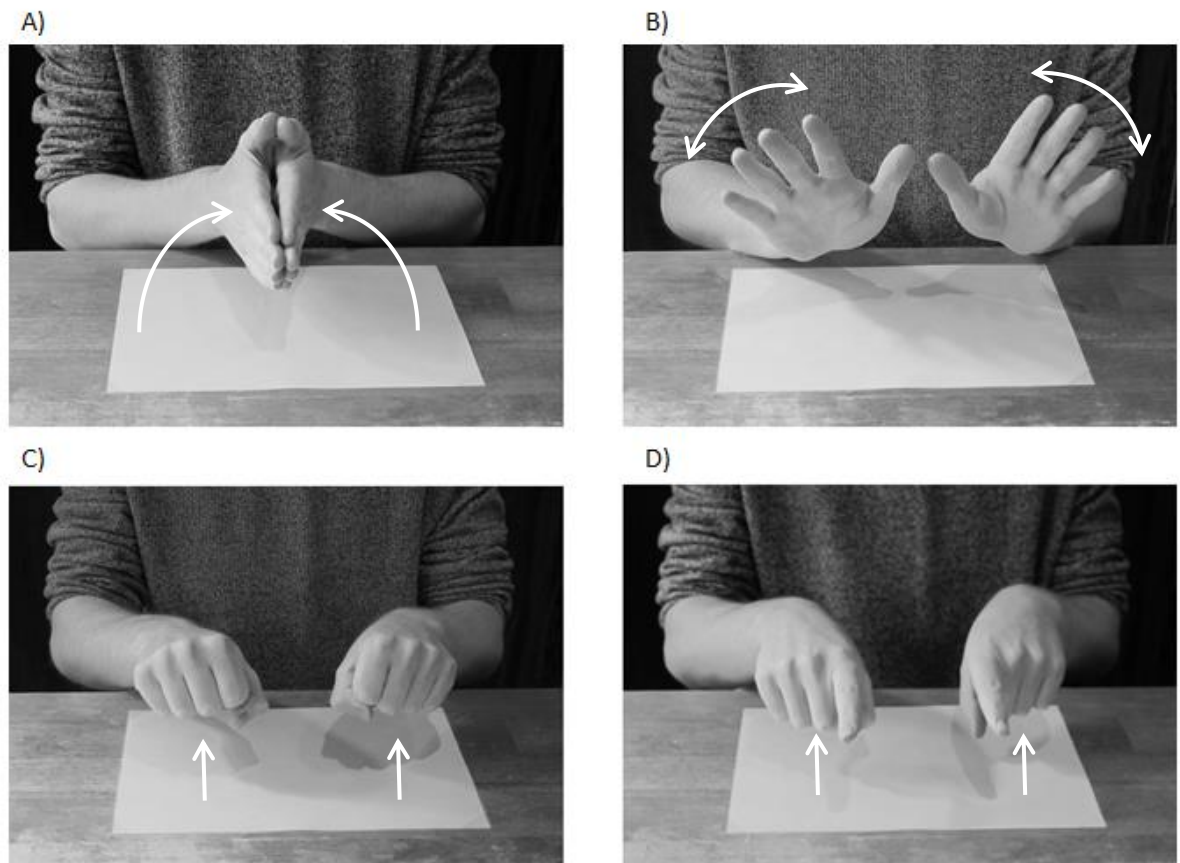
One game required the participant to watch the actions of the experimenter and perform with the same action (compatible response rule), and the other game required the participant to perform the alternate action (incompatible response rule). To be included in the analysis a participant had to complete both actions sets with both response rules. The order of the games was counterbalanced for both response rule and action set.

Procedure

During a research session the experimenter and participant sat facing each other across a table. Two sheets of A4 paper were attached to the table in front of both the participant and the experimenter (see Figure 3.3). At the beginning of the session the experimenter explained that a game was to be played and to begin the child must place their hands flat on the sheet of paper (see Figure 3.3). The experimenter demonstrated the two actions to be performed in the first game and asked the participant if they were able to perform each of the two actions: E.g. "Can you wave your hands like this". Next, the experimenter explained the response rule for each of the two actions and asked the participant to demonstrate a response: E.g. "In this game if you see me wave my hands (*experimenter waves his hands*), you do the different action, the opposite action, and you clap your hands (*experimenter claps his hands*). So, if I do this (*experimenter waves his hands*) what do you do?" After explaining the response rules for both actions the participants' understanding of the rules were tested by asking the child to respond to both actions in order. If the participant performed an incorrect response the rules were repeated and a further two trials tested comprehension. Correct responses during this pre-test phase were rewarded with verbal praise, and if both responses were correct the child progressed to the testing phase. If the child did not perform two consecutive correct responses after four pre-test trials the child progressed to

the testing phase nonetheless. If these children passed the criteria for inclusion (see below), their data was included in the analysis.

Figure 3.3. Starting position for both experimenter and participant at the beginning of each trial.

The testing phase consisted of ten response trials presented in a pseudorandomised order. Children were told to react as quickly as possible. To begin a trial both experimenter and participant placed their hands flat on the sheet of paper (see Figure 3.2); if the child did not have their hands on the paper they were prompted to do so (e.g. "hands flat", "hands on the paper"). The experimenter would rapidly perform an action, return his hands to the starting position, and wait for the child to respond. During this testing phase

correct responses were not praised and incorrect responses were not corrected by the experimenter. If an incorrect action was performed the experimenter would wait approximately two seconds for the child to change their action. Between trials (correct and incorrect), children were encouraged to prepare themselves for the next trials with various verbal cues including "hands flat", "ready", and "next one". After the tenth trial the child was praised for his or her performance, and told that the game was to be played again but with the rules changed around. The procedure described above was then repeated but with the response rules reversed. After completing ten test trials with both response rules, the same overall process was repeated with the different action set.

Video Coding

Videos were coded at a normal playing speed until a trial occurred- then the video was coded frame-by-frame to measure reaction time. Each session was recorded at 25 frames per second (fps; interlaced). Interlaced video allows for greater temporal resolution by overlapping adjacent frames to create a perceived resolution of 50 frames per second. The videos were coded at this higher rate of temporal resolution, and measurements are reported as such.

The response to each stimulus was coded as being correct or incorrect. If a participant's response was incorrect initially but corrected before the next action was performed by the experimenter, the response was coded as being correct and the initial mistake was noted and pooled with other, uncorrected incorrect responses. A measure of reaction time started once an action was completed by the experimenter and ended once the completion criteria was met by the participant (see Table 1 for definitions of action completion). As actions were sometimes performed quicker by one of the participant's hands, the measurement of reaction time ended once the action was completed by one hand in the case of all actions other than clapping.

Data analyses

To be included in the analyses participants had to perform correct responses on 60% of trials within each game (i.e. for each response rule for both actions sets). This criterion was used to ensure that each participant had understood the rules of each condition. For the purpose of analyses, each participant's overall performance was summarised to include the number of correct responses in each condition (including corrected trials), the number of mistakes made in each condition, and the average reaction time for each condition.

Table 3.1. Definitions used to begin and end a measurement of reaction time on a given trial.

Action	Action Completion Criteria
Wave	Hands first change direction of movement (i.e. if hands were moving inwards, measurement began once hands began moving away from each other)
Clap	Hands make contact.
Point	Pointing finger visibly extended from the rest of the fingers
Close hand	Fingers are closed and pressed into the palm

It is worth noting that the correct responses and mistakes are not inverse measurements, as a mistake can be corrected within a trial. For example, during a counter imitative session a participant might quickly imitate on five trials before correcting themselves to perform the correct response on each of the five trials. This participant's summarised performance for that session would include 10 correct responses and 5 mistakes. Participants' average reaction time for each condition was a measurement of their mean reaction time following removal of any outlying responses (± 2 standard deviations of original mean, 3.6% of total trials).

Statistical Software

All statistical analyses were performed in SPSS 19 and all figures and graphs were produced using R (R Core Team, 2014) in the Rstudio environment (RStudio Team, 2014) using the ggplot2 package (Wickham, 2009). For repeated measures tests with more than two conditions Mauchly's test of sphericity was performed and necessary adjustments were made based on Field (2013).

Results

To examine the overall effect of the two response rules and two action sets on reaction time (RT) a 2X2 repeated-measures analysis of variance (ANOVA) was applied. A main effect of response rule was identified ($F(1, 71)= 464.405$, $p <.001$) with a mean difference of 28.62 frames between compatible and incompatible rules (standard error, SE = 1.328; see Figure 3.4). Also, a main effect of action set was found ($F(1, 71)= 5.698$, $p = .02$) with a mean difference of 3.182 frames (SE = 1.33) in RT between the CIS (mean = 55.67) and the RIS (mean = 52.49; see Figure 3.4). A significant interaction between action set and response rule was also identified ($F(1,71)=25.631$, $p <.001$). Post-hoc contrasts with Bonferonni correction identified significantly faster reaction times to incompatible response rules in the RIS than the CIS (mean difference = 8.262, SE = 1.879, $p <.001$), but no significant difference between compatible rules (mean difference = 1.898 frames, SE = 1.428, $p = 1$). We calculated an automatic

imitation score (AI score) for each set of actions by subtracting the average

participant RT on compatible trials from average RT on incompatible trials.

This score represents the average difference in RT between compatible and

incompatible trials. Comparing scores from both action sets using a repeated-

measures t-test identified a significant difference, with smaller AI scores in the

RIS (mean = 23.54, SE = 1.54) than in the CIS (mean = 33.70, SE = 1.78; t(71) =

5.061, p<.001).

Figure 3.4. Mean reaction time to each response rule (compatible and incompatible), and each action set (Commonly Imitated Set and Rarely Imitated Set). Error bars represent standard error of the mean.
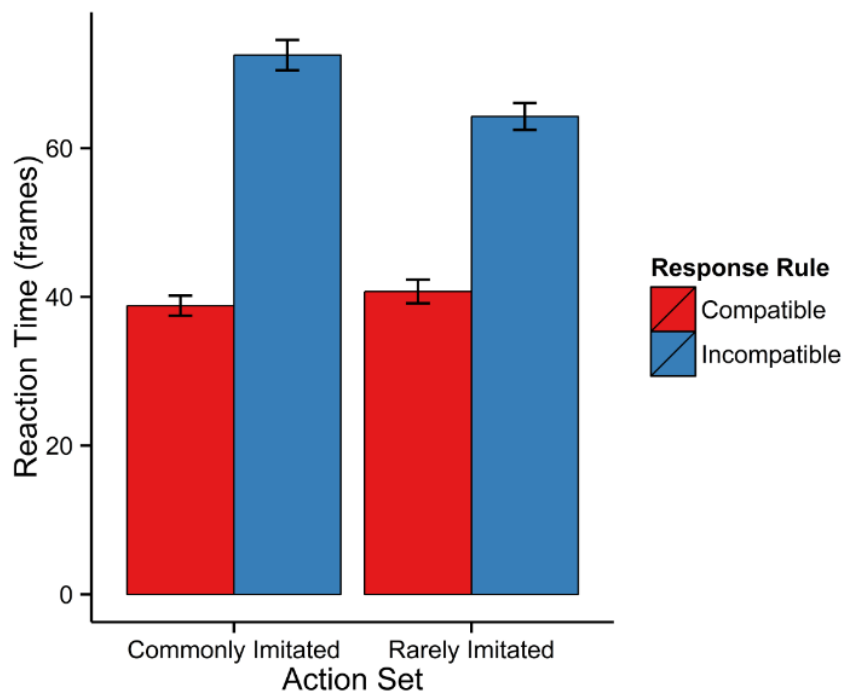
A similar analysis was conducted to examine the effect of action set and response rule on the number of mistakes out of the total of 10 trials per participant for each condition. A 2X2 ANOVA identified a significant main effect of response rule (F(1, 71) 22.05, p <.001) with significantly fewer mistakes made when responding to the compatible rule (mean = 1.132, SE = 0.113) than the incompatible rule (mean= 1.854, SE = 0.163).

A significant main effect of action set was also found (F(1,71) = 51.2, p<.001) with more mistakes made in the RIS (mean= 2.083, SE= .172) than in the CIS (mean= .903, SE=.106). There was no significant interaction between action set and response rule (F(71, 1)= .157, p = .639). Post-hoc comparisons with Bonferonni corrections identified fewer mistakes when reacting to compatible conditions in the CIS (mean = .513, SE = .086) compared to incompatible responses in the CIS (mean = 1.292, SE = .174, p <.001), and both response rules in the RIS (mean$_{compatible}$= 1.75, SE$_{compatible}$= .198, p<.001; mean$_{incompatible}$= 2.42, SE$_{incompatible}$= .220, p <.001). Significantly fewer mistakes were made in response to incompatible rules in the CIS than incompatible rules in the RIS (p<.001), and within the RIS more mistakes were made when responding to incompatible rules (p = .039). An AI effect based on mistakes was calculated for each action set by subtracting the mistakes made to compatible response rules from mistakes made to incompatible response rules. There was no difference

110

between the AI effects for the CIS (mean = .778, SE = .174) and the RIS (mean = .667, SE = .237, t(71) = .397, p=.693).

Stimuli Effects

We examined effects of specific stimuli by examining reaction times upon presentation of each action stimulus for both rules. We performed two one-way repeated measures ANOVAs, one for compatible rules and one for incompatible rules, with action stimulus as the independent variable. In both cases, Mauchly's tests indicated that the assumption of sphericity was violated ($X^2(5)_{compatible}$=49.09, p<.001; $X^2(5)_{incompatible}$=19.03, p=.002), so degrees of freedom were corrected using Greenhouse-Geisser estimates for compatible actions (ε=.713), and Huynh-Feldt estimates for incompatible actions (ε=.837; see Field, 2013). We found a marginally significant main effect of stimulus type for compatible responses (F(2.14, 151.77)=2.891, p = .055; see Figure 3.5), and a significant effect of stimulus type for incompatible responses (F(2.61, 185.426)= 11.301, p<.001, see Figure 3.5).

When responding with compatible actions, post-hoc tests with Bonferonni corrections identified significantly quicker RTs to clapping (mean= 37.704, SE = 1.50) than waving (mean = 41.309, SE = 1.36; p = .002) and marginally

significantly quicker RTs to pointing (mean = 41.899, SE = 1.794; p= .060), but no

other significant difference were identified between other actions.

Figure 3.5. Mean RT to specific actions for both response rules. Error bars represent the standard error of the mean.
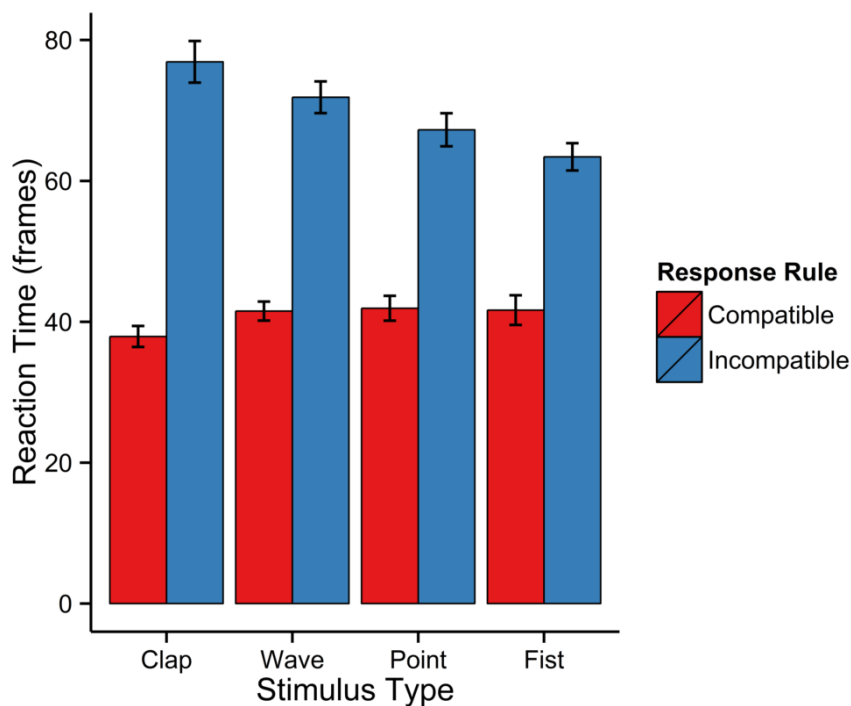
For incompatible response rules post-hoc tests with Bonferonni corrections

identified significant slower RT to clapping (mean= 76.91, SE = 2.95) than

pointing (mean = 67.257, SE = 2.34; p = .009) and hand closing (mean = 63.413,

SE = 1.938; p<.001), but no significant difference between clapping and waving

(mean = 71.876, SE = 2.252; p = .219). Post-hoc comparisons also identified

significantly longer RTs to waving stimuli than to hand closing stimuli (p = .002).

Figure 3.6. Mean automatic imitation scores for each of the four actions (i.e. difference between RT to compatible and incompatible response rules) . Error-bars represent standard error of the mean.
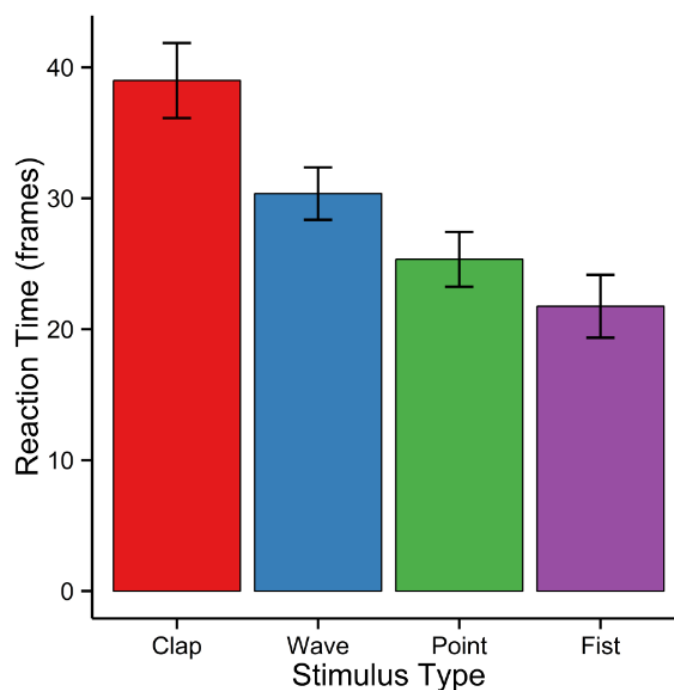
Examining differences in automatic imitation effects for each action stimulus (i.e. subtracting RT for compatible responses from RT for incompatible responses) identified a significant effect of stimulus (F(2.84, 201.994)=13.224, p <.001; Mauchly's test indicated that the assumption of sphericity was violated so degrees of freedom were corrected using Huynh-Feldt estimates, ε=.948).

113

Post-hoc comparisons with Bonferonni corrections identified the AI effect for clapping (mean = 38.99, SE = 2.87) was significantly greater than the AI effect for waving (mean = 30.36, SE = 2.00; p = .013), pointing (mean = 25.336, SE = 2.092; p <.001), and hand closing (mean = 21.753, SE = 2.404; p <.001; see Figure 3.6). Waving had a significantly greater AI effect than hand closing (p=.025), and there was no difference in AI effect between pointing and waving (p = .195) and between pointing and hand-closing (p= 1).

Order Effects

We examined whether the order that response rules were completed had an effect on automatic imitation. The order of presentation had no influence on the AI effect for commonly imitated actions (t(70) = -1.109, p=.271; see Figure 3.7). However, a significantly greater AI effect was found for rarely imitated actions when the compatible response rule was first (mean = 27.13. SE = 1.67; t(70) = -2.471, p=.016; see Figure 3.7) rather than when it followed the incompatible response rule (mean = 19.79, SE = 2.50). However, this reduced AI effect was still significantly different from zero (t(35) = 8.14, p<.001).

Figure 3.7. Mean automatic imitation effects for both action sets comparing sessions where compatible rule trials took place before incompatible rules (red) and when compatible trials followed incompatible trials (blue). Error-bars represent standard error of the mean.
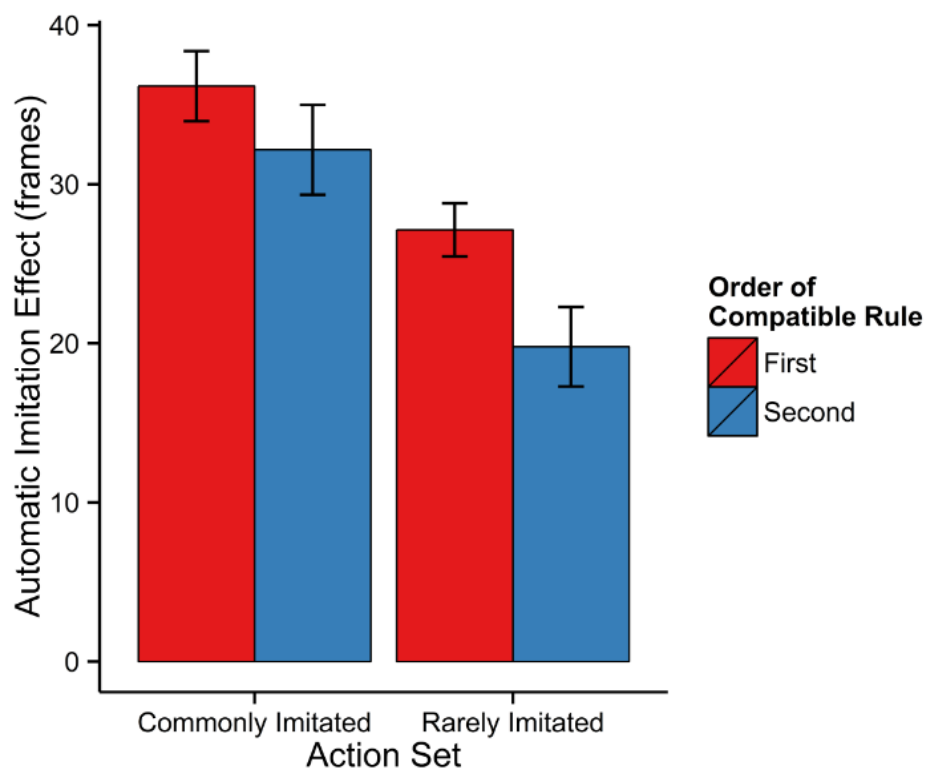
Age effects

Examining the effect of age on reaction times to imitative rules identified a significant negative relationship between RT and age for both action conditions (r_{cis}= -.486, p <.001; r_{ris}=-.486, p <.001, see Figure 3.8A). We also found that age was negatively correlated with RTs to incompatible rules for both action sets (r_{cis}= -.435, p <.001; r_{ris}=-.453, p <.001, see Figure 3.8B). Age was unrelated to

automatic imitation effects in either action condition (r_{cis}= -.132, p =.271; r_{ris}=-.032, p =.791).

Figure 3.8: Participant's average reaction time as a function of age when responding in (A) compatible trials and (B) incompatible trials for both commonly imitated actions (in red) and rarely imitated actions (in blue). Lines represent the linear regression lines for the predicted effect of age on reaction time for each condition and action set.
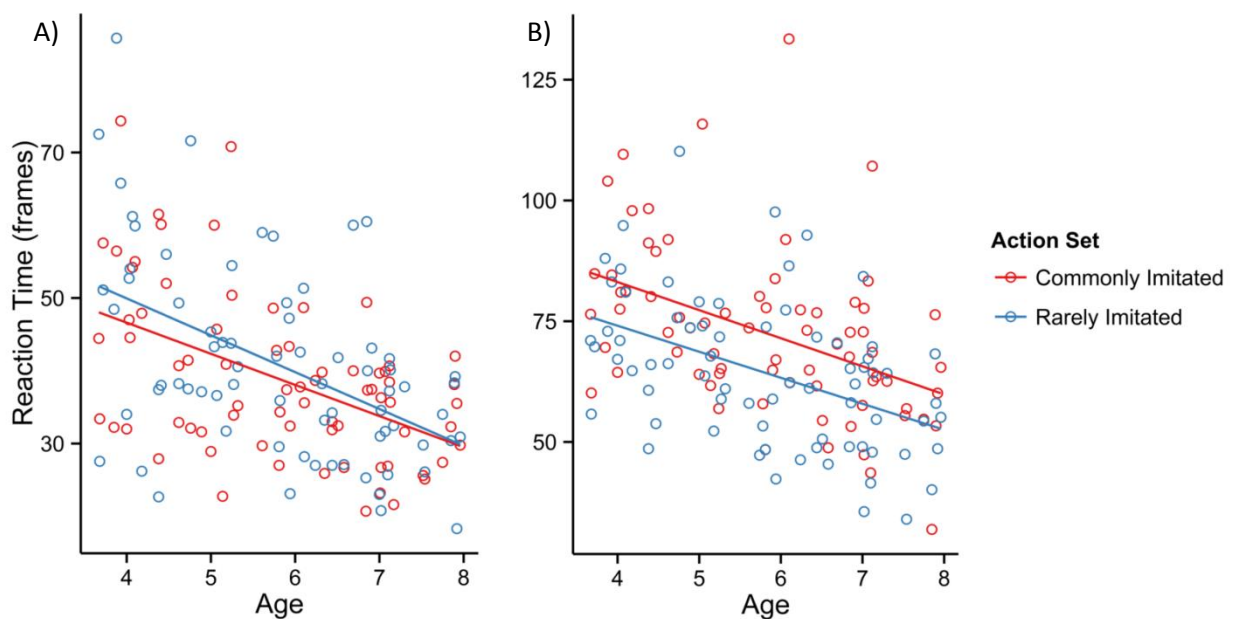
Having identified a significant difference between the automatic imitation effects for commonly imitated and rarely imitated action sets, we examined whether there was any relationship between age and this effect. With this goal in mind, a "prior experience score" was measured for each participant by

subtracting the average AI effect for rarely imitated action from their score for commonly imitated actions. This score represents the average difference in AI effect between action sets for each participant (a positive score represents a greater AI effect for the CIS, a negative score represents a greater AI effect for the RIS). We found no effect of age on this prior experience score (r = -.092, p=.440).

Discussion

This study of automatic imitation is the first to specifically test predictions of the ASL model of imitation in children. Unsurprisingly, given the impressive imitative skills of children from the age of three we found a significant automatic imitation for both sets of actions (see Figure 3.4). However, it is the difference in automatic imitation effects between action sets that is of the most interest. The ASL model, as well as the ideomotor approach, predicts that associations between sensory and motor representations of actions are formed through experience and so actions that receive more of this sensorimotor experience should be quicker to imitate and more difficult to inhibit. Commonly imitated actions were not imitated quicker than rarely imitated actions. However, incompatible responses to commonly imitated actions were slower than incompatible responses in the rarely imitated action set. This resulted in an overall difference in automatic imitation between actions sets

with a greater automatic imitation effect identified in the commonly imitated set. This finding supports the ASL view of the development of imitation, demonstrating that sensorimotor experience facilitates associations between sensory and motor representations of an action aiding imitation, and interfering with the inhibition of a learned response.

Further evidence in support of a domain-general account is provided by our finding that clapping stimuli generated the strongest automatic imitation effect, an observation that is predicted by the ASL model's account of environmental stimuli facilitating the connection between sensory and motor representation of an action. Environmental stimuli are thought to bridge cognitive representations in cases where actions may not provide sensory feedback (Ray & Heyes, 2011); however, they may also act to strengthen associations for observed actions. This corresponds with evidence of audio-visual mirror neurons identified in monkeys that fire when performing an action, seeing an action, and hearing an action (Keysers et al., 2003). If automatic imitation is indeed a behavioural effect of mirror neuron activity formed through associative processes, we would expect this more pronounced effect when motor actions have become associated with multiple stimuli across different modalities. While it is known that reaction times to multisensory stimuli are quicker than reaction times to a single stimulus (Andreassi & Greco, 1975;

Hershenson, 1962), here, we only observe quicker reaction times when responding with a compatible action suggesting a compatibility-specific effect (although this compatibility effect is only marginally significant). If reaction times were quicker for both compatible and incompatible trials, we could conclude that bimodal stimulation may be the determining factor, however, a significant decrease in reaction time to bimodal clapping stimuli was observed in counter imitative trials. To my knowledge, studies of the effects of bimodal stimuli presentation have not examined inhibition of prepotent responses to bimodal stimuli and whether this effect is greater than responses to unimodal stimuli. It is also possible that of all the actions used as stimuli, clapping is by chance the action performed in synchrony the most often, leading to the observed effect. This interpretation, while compatible with the ASL view of imitation, incorporates a conceptually different mechanism. Future studies could easily differentiate between these two interpretations by manipulating the degree of experience participants receive as well as the degree of intermodal sensory information available during learning and subsequent inhibition of responses to novel associative stimuli. This protocol could isolate the role of both experience and stimulus complexity in imitative learning.

Partial support for the ASL view of imitation is found when examining the effect of counter-imitative experience preceding imitative action. In rarely

imitated action sets it was found that a short session of counter-imitative training significantly reduced the automatic imitation effect. Previous research has eliminated automatic imitation effects entirely through counter-imitative training (Heyes et al., 2005), while here we merely reduce it. However, the training received in this study (approximately 12 trials) is not comparable to the training in other studies (e.g. 6 blocks of 72 trials, Heyes et al., 2005). While a similar order effect was not observed in the commonly imitated action set, this may not be surprising given our assumption that commonly imitated actions will have stronger sensory-motor connections that may require more extensive training to alter. Overall, while simple order effects are common in experimental paradigms of this sort, the point highlighted here is that imitative compatibility effects are not immune to such effects.

While it was found that older participants averaged quicker RTs for both response rules within each action set, no change in automatic imitation was found. This is not necessarily surprising. Based on the ASL approach one might predict that an automatic imitation effect would increase with age as cumulative sensorimotor experience would lead to increased inter-representational connectivity. However, in the paradigm explored here we are dealing with two effects: An imitation effect and an inhibitory effect. To react to an action stimulus with a different action one must inhibit imitation. Evidence

from previous studies of inhibition in children have found that the ability to inhibit prepotent responses increases with age (Simpson & Riggs, 2011). With this in mind, as children age we might expect that experience would contribute to greater sensorimotor co-ordination resulting in quicker reaction times in imitative trials, and developing inhibitory control should reduce RTs when responding to incompatible stimuli. If this is the case it is not surprising that we see a consistent automatic imitation effect throughout development.

It could be argued that the automatic imitation effect reported here is solely a result of a higher memory load required to react to incompatible rules (i.e. the "different action" has to be remembered for an incompatible rule, while this information is readily available in the stimulus in the compatible condition), however, previous research on inhibition has concluded that memory alone does not account for the difficulty children face when reacting to stimuli that are incompatible with the action to be performed (Gerstadt, Hong, & Diamond, 1994; Simpson et al., 2012). Many studies have examined children's responses on day-night tasks. In these tasks, participants are presented with a stimulus picture that is usually incompatible with a response; e.g. if the stimulus shows a picture of a sun the response is to say the word "moon". Researchers have shown that increased memory load is not the only effect contributing to inhibitory responses (Simpson & Riggs, 2011; Gerstadt et al., 1994). Under the

present paradigm automatic imitation is likely to function in conjunction with working memory and other inhibitory effects, but as this study is more interested in examining automatic imitation in different contexts where memory load and inhibitory context is kept constant, this interaction does not affect our conclusions. Nonetheless, future studies with children should attempt to isolate automatic imitation effects.

The goal of this chapter was to examine imitation from a developmental perspective. While early work in the field attempted a detailed description of a stepwise development of imitation in infancy (Piaget, 1951/1962), recent work on this subject is sparse. It is crucial to consider developmental approaches to imitation as even an innate imitative system must interact with the environment to generate adaptive behavioural responses. From this perspective an associative model complements innate dispositions. In fact, to account for the vast difference in imitative ability between humans and other animals (e.g. Whiten, Horner, & Marshall-pescini, 2005) the ASL approach must recognise innate differences in motivation or attention to account for the unique routes human development takes (Heyes, 2012b). The strength of a good theory rests on the reliability and validity of its predictions. There is no doubt that the ASL model of imitation has need for further empirical support, but converging evidence from cognitive (Heyes et al., 2005), neuroscientific (Catmur et al.,

2008), comparative (Range & Huber, 2007), and now developmental fields suggests that this model is reliable in varied contexts. Future research will be necessary to examine the predictive power of this model in younger children than are still developing their imitative skills. This study marks a first step towards realising that goal with an older sample. Furthermore, while there is much debate over the function of mirror neurons (Gallese et al., 2011; Rizzolatti & Craighero, 2004; Wicker et al., 2003), an associative account suggests that mirror neurons may be by-products of sociality, an exaptation instead of an adaptation (Cook et al., 2014). Future research will explore the importance of an ASL model to social learning and mirror neurons, but now social learning will be considered from a different perspective. In the next chapter, we will take a step back and examine social learning at the group-level.

Chapter 4: Exploring three levels of social influence in capuchin monkeys

Social animals will adapt and adjust their behaviour in response to cues from conspecifics. Sometimes, a social cue may lead to a string of cognitively demanding processes resulting in behavioural change (e.g. hierarchical imitation; Byrne & Russon, 1998), but socially influenced action is also elicited by simpler, implicit processes (Bargh & Chartrand, 1999; Frith & Frith, 2008). Implicit forms of social influence are observed when humans form bidirectional paths on crowded streets (Helbing, Buzna, Johansson, & Werner, 2005), and when baboons co-ordinate their movement through their foraging ranges (Strandburg-Peshkin et al., 2015). Social influence occurs when the mere presence of others increases feeding rates (Decastro, 1994; Galloway, Addessi, Fragaszy, & Visalberghi, 2005), and when the emotionally valenced calls from neighbouring conspecifics induces behavioural change (Watson & Caldwell, 2010). These simpler and likely more automatic processes may not receive the same empirical attention as processes thought to require more complex brainpower, but their influence on both human and nonhuman behaviour is pervasive. The objective of this chapter is to highlight certain forms of social influence considered to be less cognitively demanding and explore their effects in a captive population of primates.

Group-level behavioural synchrony is under-studied in the primate literature. The study of co-ordinated or synchronous behaviour in non-human primates tends to focus on coordinated-action at the dyadic level (e.g. Fichtel, Pyritz, & Kappeler, 2011; Fuhrmann, Ravignani, Marshall-Pescini, & Whiten, 2014), ignoring the complexity of the dynamic social-space many animals inhabit. The empirical study of what has become known as "collective behaviour" is currently flourishing in non-primate fields with the support of rigorous mathematical modelling of group-systems (Faria et al., 2010; Simpson, Raubenheimer, Charleston, & Clissold, 2010). Couzin (2007) has argued that the rules that govern collective behaviour may allow individuals to tap into "higher-order collective computational capabilities" (p. 715) that may in turn allow optimum decision making about where to forage, when to move, etc. The superior wisdom of crowds in some situations has been long established in humans (e.g. Galton, 1907), but it is only recently that this effect has been studied in nonhuman animals. Modelling the movement of shoals and flocks has revealed that seemingly complex co-ordinated and adaptive movement is likely driven by simple behavioural rules enacted on the individual level (Berdahl, Torney, Ioannou, Faria, & Couzin, 2013; Couzin, Krause, James, Ruxton, & Franks, 2002). For example, flocks of starlings (*Sturnus vulgaris*) use simple heuristics to form intricate flight patterns (Carere et al., 2009). Similarly co-ordinated movement has been reported in fish (Rosenthal, Twomey, Hartnett, Wu, & Couzin, 2015), and other bird species (Beauchamp, 2012).

Examination of group-level behavioural effects in nonhuman primates is also a more recent development.

The study of behavioural synchrony in primates has primarily examined the influence of *individuals* on group movement (e.g. King, Sueur, Huchard, & Cowlishaw, 2011; Petit, Gautrais, Leca, Theraulaz, & Deneubourg, 2009; Sueur, Deneubourg, & Petit, 2012). One study of chacma baboons (*Papio ursinus*), however, has taken a broader approach to examining group-level synchrony. King & Cowlishaw (2009) used a measure of species diversity (Simpson's Diversity Index, Simpson, 1949, cited in King and Cowlishaw, 2009) to examine behavioural diversity in baboon troops. Higher scores on this measure correspond to less behavioural diversity, and greater behavioural synchrony. This measure of group synchrony allowed the authors to test a variety of hypotheses concerning ecological and social predictors of group synchrony. For example, greater synchrony was found to occur in more cohesive groups (i.e. groups spread over a smaller area). This finding may reflect the mediating role proximity might play in facilitating instances of social influence, by increasing the perceptual availability of social cues. King and Cowlishaw also identified a reduction in synchrony in larger groups, an effect that may be relevant in the broader context of social facilitation effects mediated by group-size.

Social facilitation occurs when the "sheer presence of other individuals" influences behaviour (Zajonc, 1965, p. 269). This simple effect has been primarily studied in the domain of social psychology where the presence of other human observers has been found to both facilitate and impede behavioural responses. Reviewing the literature on the topic, Zajonc (1965) notes a consistent pattern in the way the presence of observers affects behaviours. When an individual is performing a well-rehearsed behaviour (e.g. attending to a stimulus, completing a simple maths task), the presence of others seems to enhance the performance of the behaviour. However, a behaviour that is more cognitively demanding (e.g. learning series of nonsense syllables) is hindered by an audience (Zajonc & Sales, 1966). Recent studies have validated these findings in humans (Bowman, Weber, Tamborini, & Sherry, 2013; Garcia-Marques, Fernandes, Fonseca, & Prada, 2015), and social facilitation of well-rehearsed behaviours has also been noted in many animals. For example, the social facilitation of eating behaviour is documented in chickens (Tolman, 1964), rats (Harlow, 1932), and monkeys (*Cebus apella*; Galloway et al., 2005). However, as discussed in Chapter One, the influence of presence varies depending on the number of conspecifics nearby.

It is thought that one of the benefits of group living is that the group can share the responsibility of vigilance for predators, thus reducing the need for

individual vigilance to the benefit of other behaviour such as foraging. Indeed, in many species individuals are found to spend less time scanning their environment when in larger groups (Ebensperger, Hurtado, & Ramos-Jiliberto, 2006; Pays et al., 2009; for review see Roberts, 1996). Conversely however, studies of primates have not replicated the same relationship between group-size and vigilance (Hirsch, 2002; Treves, 1998, 1999). For example, one study of brown capuchin monkeys found that a greater number of conspecifics within 10 metres of a focal individual actually led to increased vigilance behaviour (Hirsch, 2002). In these cases, it is thought that vigilance functions to monitor conspecifics and not predators. Interestingly, this negative association between group-size and individual vigilance has also been found in carrion crows (*Corvus corone*; Robinette & Ha, 2001), a species that share many socio-cognitive characteristics with capuchin monkeys (e.g. large brain relative to body, Macphail, 1982; high tolerance of conspecifics, Miller, Schiestl, Whiten, Schwab, & Bugnyar, 2014). Larger group-size has also been found to facilitate foraging behaviour (e.g. Beauchamp, 2013; Ebensperger et al., 2006; Pays et al., 2009), but this has not yet been studied in primates. These group-size effects are another facet of group-level social influence that is often ignored in the primate literature.

Furthermore, the reach of social influence does not end within a group. The

behaviour of individuals within one captive group has been found to influence the behaviour of those in another group as long as auditory and/or visual contact is available. This phenomenon is known as the neighbour effect and while it is likely to occur in wild populations, it has been mostly studied in captive primate groups (Baker & Aureli, 1996; Videan et al., 2005; Watson & Caldwell, 2010). Baker and Aureli (1996) found that when aggressive calls were made by neighbouring groups of chimpanzees (*Pan troglodytes)*, the focal group would be more likely to perform aggressive behaviours. A more recent study found that affiliative behaviours were similarly affected by neighbouring group vocalisations (Videan et al., 2005). Common marmosets (*Callithrix jacchus*) showed increased levels of affiliative behaviours when vocalisations from a neighbouring captive group were affiliative, while rates of aggression increased when neighbouring groups emitted vocalisations related to negative or aggressive states (Watson & Caldwell, 2010). More recently, a study examined this effect experimentally, discovering that an increase in affiliative behaviours could be induced through playback of affiliative vocalisations (Watson et al., 2014). The neighbour effect extends the reach of social influence beyond the boundaries of a single conspecific group, and while not yet studied, it is likely that this effect also applies to neighbouring groups of different species, especially when those species form close associations. This review of neighbour effects in primates completes this overview of some of the social phenomena that may influence individual behaviour in the context of group living, all of

which will be examined empirically in this chapter.

Here, I report an investigation of three forms of social influence. The Living Links Research Centre's neighbouring outdoor enclosures, containing separate populations of capuchin monkeys, create an opportunity to examine both inter- and intra- group dynamics. Data collected from scan samples of both groups of capuchin monkeys allowed the inspection of factors that contribute to within-group behavioural synchronisation, as well as the influence of group-size on behaviour. Furthermore, by collecting simultaneous scan samples of each captive group we were able to study neighbour effects. The overarching aim of this study was to examine social influence at the group level, and predictions were generated based on previous literature.

The work of King and Cowlishaw (2009) is the only previous study of non-human primates to examine behavioural synchrony at the group level and so this work formed the basis for predictions. Their study identified spatial proximity as a predictor of increased behavioural synchrony. In the research reported in this chapter, the location of a group acted as a proxy measure of spatial proximity. The indoor enclosure at Living Links are considerably smaller (30m²) than the outdoor enclosure (900m²), and so the same number of

monkeys located in an inside enclosure are therefore closer to each other on average. It was predicted that behavioural synchrony would be greater indoors in more cohesive groups (prediction 1). King and Cowlishaw (2009), also found that smaller groups were more likely to be synchronous in their behaviour, an effect attributed to a smaller number of individuals displaying a less diverse range of behaviours. Based on this finding, it was predicted that smaller groups would be more synchronised in their behaviour on average (prediction 2). As this is the first study of behavioural synchronisation with captive primates no further predictions concerning the effects of environmental factors were made, however, the contribution of a number of environmental factors were considered.

It was expected that group size would influence the likelihood of certain behaviours being performed. Evidence that rates of vigilance in wild capuchins are positively correlated with group size (Hirsch, 2002) led to the prediction of a similar effect being identified in our captive sample (prediction 3). No previous study of primate behaviour has examined the relationship between group size and foraging behaviour. However, based on studies of other mammals (Ebensperger et al., 2006; Pays et al., 2009) it was predicted that rates of foraging behaviour would increase with group-size (prediction 4). While feeding behaviours are normally influenced by social facilitation, this effect was

not examined here as captive feeding schedules confound an examination of influencing social factors. No further *a priori* hypotheses were made concerning the effect of group size on behaviour but the relationships between this variable and all behaviours measured was examined.

The two separate monkey troops in the Living Links research site have auditory and visual contact with each other (see methods for further details). Based on previous findings of the influence of neighbouring groups on the transmission of aggressive and affiliative behaviours in New World monkeys and apes (Videan et al., 2005; Watson & Caldwell, 2010), it was predicted that behaviours associated with affiliation and relaxed contexts (grooming, play, resting) would be correlated between groups (prediction 5). Aggressive behaviour was not directly measured in this study (due to the difficulty in capturing short duration aggressive behaviours through instantaneous scan sampling methods). However, measures of vigilance and locomotion were used as proxy measures of anxiety or unease in the group. It was predicted that the incidence of these behaviours would be correlated between both groups of monkeys (prediction 6). By studying a range of factors thought to socially influence primate behaviour it was hoped that a better understanding of the connections between the multiple levels of explanation would be achieved.

Methods

Animals and research site

This study was conducted at the Living Links to Human Evolution Field Site at Edinburgh Zoo (Living Links). As mentioned in Chapter Two, this research facility houses two separate mixed-species troops of squirrel monkeys (*Saimiri scirilius*; 36 individuals) and capuchin monkeys (*Sapajus sp.*; 27 individuals). Capuchin and squirrel monkeys form mixed species groups in the wild and research at the Living Links site discovered that the smaller of the two species chose to interact with capuchins and no evidence of chronic stress induced by mixed species interactions was identified (Leonardi, Buchanan-Smith, Dufour, MacDonald, & Whiten, 2010). Each mixed species group inhabits a separate enclosure named the East and West wings (see Figure 4.1; for a more complete overview of the site see Leonardi et al., 2010). Each mixed species group shares an outdoor enclosure measuring approximately 900m², and each species has their own inner enclosure. The capuchin inner enclosure measures 31.5m² and the squirrel monkey enclosure measures 24.75m²; both inner enclosures are 6m high. The squirrel monkeys are able to enter the capuchin inner enclosure, but capuchins cannot enter squirrel monkey enclosures. Primary feedings of fruit and vegetables occur twice daily (occasional feedings of insects and other protein), and additional scatter feeds also take place regularly. Food is regularly

delivered through enrichment devices. Ethical approval was granted for this study by the University of Stirling, Psychology Ethics committee.

Figure 4.1: Schematic representing a plan-view of the Living Links to Human Evolution Research Site, taken and adapted from Leonardi et al., 2010).
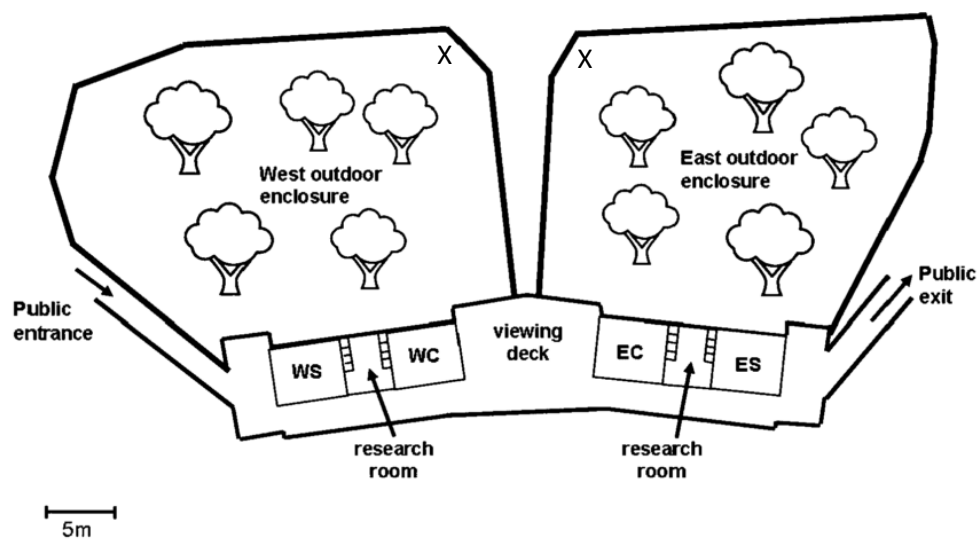
Behavioural sampling

Within-group and between-group social influence was examined through scan sampling methods (Martin & Bateson, 2007). Scans were made of both captive capuchin troops simultaneously by two researchers. Squirrel monkeys were present during many sampling points but their presence was not recorded. All capuchin monkeys were sampled in each scan, including infants. However, four infants under the age of one year (two from each troop) were subsequently

excluded from all analyses as some behaviours were infant-specific (e.g. being carried by a parent) and were not relevant when examining group-level behaviour. Behavioural observations were made between 23.08.13 and 3.10.13, and took place between 9am and 6pm. Time of observation was recorded, as well as weather conditions (cloudy, sunny, or raining). Relevant details were recorded concurrently by both researchers at the beginning of each scan at the viewing deck (see Figure 4.1), and each researcher subsequently began recording data from the outdoor enclosure of either the West or East troop. The temperature at the time of the scan sample was recorded retrospectively from weatherspark.com using the closest available weather station as a reference point (Edinburgh Airport). While this discrepancy in location of temperature may mean slight absolute difference between recorded temperature and actual temperature at the research site, relative variation in temperature throughout the sampling periods should be reliable.

Once the behaviour of all monkeys in the outdoor enclosure was recorded the researcher would move to the indoor enclosure to observe the remaining individuals. Once an individual was recognised, the researcher waited 5 seconds before recording the monkey's location and the behaviour being performed (see Table 4.1). A total of 94 scans were collected for the East troop, and 93 for the West troop (uneven N per group due to incomplete data for some scans). During scans a monkey could be inside or outside. For the

purpose of analysing group-level effects, a group was then defined as two or more monkeys present in the same enclosure (i.e. inside West, inside East, outside West, and outside East), allowing the possible measurement of four "groups" at each sampling point (from our two monkey troops). Scan samples where one individual or no individual was present in a location (inside/outside) were not included in the analysis of behavioural synchrony (i.e. minimum of two individuals needed) and 254 group-scans were included in the final analysis (N_{east} = 125; 89 outside, N_{west}= 129; 78 outside). To examine social facilitation, scans where only one monkey was present in a location were also included in the analyses (N_{east} = 145; 91 outside, (N_{west}= 162; 84 outside).

While East and West enclosures are separated by 2. 4 m wooden fences and no physical contact is available between troops, monkeys nonetheless have visual and auditory contact. A walkway separates the East and West outdoor enclosures which is 5.5 metres at its widest point and 2 metres at its narrowest (at the viewing deck, see Figure 4.1). The amount of visual and auditory information available between groups varies depending on the location of individuals in the enclosures. Visual contact between monkeys is possible when monkeys are in trees as well as from the ground at the locations marked with Xs on Figure 4.1 where two gates allow visual access from ground-level. Visual access between monkeys when on the ground is otherwise not possible due to the wooden fencing.

Table 4.1: Definitions of behaviours used to examine social facilitation in capuchin monkeys; adapted from Leonardi et al. (2010).

Behaviour Name	Definition
Rest (sleep)	Individual is stationary with shoulders stooped and head down.
Stationary/Vigilant	Individual is stationary but not resting; is alert and vigilant.
Locomotion	Individual is moving in relation to its surroundings.
Fast Locomotion	Individual is moving in relation to its surroundings at a fast pace. May include leaping between branches, and jumping over obstacles.
Feeding	Individual is chewing food.
Foraging	Individual is actively searching for food with hand(s) in earth or flora.
Grooming	The monkey's hands and/or lips are drawn through the coat, skin, or teeth of another and particles are occasionally removed.
Play	Monkey engages in high activity interaction with other individuals (e.g. chase, rough and tumble, mock wrestling).

Auditory contact is also possible between groups although this is also influenced by the location of monkeys in the enclosure and the volume of a vocalisation. Anecdotally, it is possible for some vocalisations from a troop to be heard throughout the entire neighbouring enclosure as some vocalisations from East capuchins can be heard when standing at the public entrance (see Figure 4.1). Communication between groups is not only passive. Monkeys from different enclosures sometimes signal to each other from trees or from the ground at section X (see Figure 4.1), often performing threat vocalisations and/or threatening postures.

To study the neighbour effect in these groups of capuchin monkeys, simultaneous behavioural observations were compared to test whether similar behaviours were more likely to be exhibited by both groups at the same time, once other environmental factors were controlled for. To this effect, when analysing simultaneous scan samples from both groups, if no monkey was present in the outside enclosure for any of the groups, the sample at this time-point was not analysed (leaving a total N of 80). Correlations between the proportion of monkeys exhibiting each behaviour in both outdoor enclosures were produced.

Analysis

Behavioural synchrony

To examine if behavioural synchrony occurred in our sample, a measure of synchrony was calculated from the collected data and compared to a measure of synchrony calculated from a dataset generated based on monkeys behaving independent of group influence. First, the probability of a monkey performing each of the measured behaviours was calculated based on the scan data (N = 254). Using these probabilities a new dataset was randomly generated with the same number of "scan observations" as the original dataset. Some of these observations resulted in one or no observed recordings for some behaviour categories and so were not included in the calculation of a behavioural synchrony score (N = 222). For all other scans a measure of behavioural synchrony was calculated. To be included in the analysis more than one monkey had to be present in an area (inside or outside), and monkeys displaying feeding behaviour were excluded from the analysis (due to husbandry imposed synchrony). Degree of behavioural synchrony was calculated using a method described by King and Cowlishaw (2009), the Simpson's Diversity Index:

$$BS = \sum_{i=7}^{S} \frac{n_i(n_i - 1)}{N(N - 1)}$$

In this calculation, n_i is the total number of individuals partaking in a measured behaviour, and N is the number of individuals in view. Behavioural synchrony scores closer to zero indicate a diverse range of behaviours were performed in a scan, while a score of 1 indicates all monkeys were performing the same behaviour. King and Cowlishaw (2009) describe the resulting score as the probability of finding two monkeys in a sample performing the same behaviour. This measures behavioural synchrony at the group level rather than focussing on the likelihood of a focal animal performing a behaviour based on the behaviour of another (or others) in the group (e.g. Beauchamp, 2009; Engel & Lamprecht, 1997; Pays et al., 2009).

Once scores of behavioural synchrony were calculated, the variation found in both real and randomly generated samples were compared with a Levene's test to assess whether variation in behavioural synchrony in our sample differed from what would be expected by chance. Subsequently, the real and randomly generated synchrony scores were compared using a Wilcoxon signed-ranks test to assess whether average behavioural synchrony differed from what would be expected by a simple model describing monkeys behaving independently of each other.

To examine what variables contribute to behavioural synchrony a linear model (LM) was developed. Behavioural synchrony scores were transformed with a logarithmic transformation to improve the normality of the model's residual values. A backward stepwise method was used to examine the contribution of a range of factors including troop observed (categorical: East/West), weather (categorical: cloud, clear, rain), location (categorical: inside/outside), temperature (continuous), hour (continuous), and group size at time of observation (count). All predictors were first included in the model, and non-significant predictors were removed in order of least significance until only statistically significant independent variables remained. Significant contributions to the model were assessed using an F-test. Predictor variables were also examined for collinearity by examining Variance Inflation Factors (VIF) and no problematic correlations were identified (i.e. no VIF greater than 5 identified; Zuur, Ieno, Walker, Saveliev, & Smith, 2009). To test whether some behaviours were more likely to have contributed to the measure of behavioural synchrony, the relationship between synchrony scores and the frequency of monkeys performing each behaviour was examined using Kendall's tau; correlations between the frequency of all other behaviours are also reported.

Within-group social facilitation

While examining group-size effects, the proportion of individuals performing each behaviour was modelled as a dependent variable. Due to a high number of zero values for each behavioural category (i.e. it was common for no monkey to be performing the behaviour of interest in a scan), ranging from 30% (vigilance) to 92% (grooming), these outcome proportional values were transformed into binary dummy factors (i.e. behaviour present, behaviour absent). Also, locomotion and fast locomotion were combined to create a single locomotion variable. Generalised linear models (GLM) with a binomial error distribution and logit link function were developed for each behaviour examining the contribution of environmental factors and group size to the likelihood a given behaviour would be observed in a scan. Feeding was excluded from the analysis due to husbandry practices. A backwards-stepwise method was used to select environmental factors that significantly contributed to the proportion of monkeys performing each behaviour (environmental factors include: temperature, time of day, group, and weather). Variables that contributed significantly to each model are reported (with accompanying Wald-tests for significance). It was expected that group size would significantly predict the performance of behaviour in these models as the likelihood of any specific behaviour being absent increases when group size is low (e.g. 1-5 monkeys in a scan). Therefore, to provide a more valid result concerning the effect of group

size on the proportion of monkeys performing certain behaviours, further analyses were performed. The group-size variable showed a non-normal distribution with greater frequency of smallest groups and largest groups. To standardise the group-size variable, a categorical variable was created based on quartiles (1st quartile: 1-5 monkeys; 2nd quartile: 6-10 monkeys, 3rd quartile: 11-12 monkeys; 4th quartile: 13-14 monkeys). The effect of group size on each behaviour was modelled independently using a GLM with a Poisson error-distribution and logit link function. Where group-size had a significant effect on a behaviour, consecutive quartiles were compared with corrected p-values (Shaffer corrections; Shaffer, 1986).

Between-group neighbour effect

Scan samples taken at the same time-point were compared in order to examine behavioural contagion between the two groups of captive capuchin monkeys. As the proportion of behaviours exhibited was highly skewed by multiple zeros, non-parametric tests were used to examine significant correlated behaviours in the East and West groups of capuchin monkeys (Spearman rho). To control for other factors capable of influencing these behaviours other variables were partialled out of the correlation (temperature, time of day, and total sum of both groups present at the time of scan). All statistics report two-tailed significance levels unless stated otherwise.

Software

All statistical tests were performed using the R software package in the Rstudio environment (RStudio, 2014; R Core Team, 2014). GLMs were performed using the lme4 package (Bates et al., 2015) and graphics were produced using the ggplot2 package (Wickham, 2009).

Results

Behavioural Synchrony

A Levene's test found a significant difference between the variability of behavioural synchrony scores based on the collected data and the data generated based on individuals acting independently (Levene's test = 51.135, p <.0001). A Wilcoxon rank-sum test identified a higher level of behavioural synchrony in the real sample (mean = .427, standard deviation, SD = .273) than the generated sample (mean = .257, SD = .132; W = 411, p<.0001). An LM examining the influence of location identified a marginally significant increase in synchrony when outside (LM: $F_{1,252}$ = 3.402, p = .066), and an LM looking solely at the influence of group size identified a positive relationship between group size and behavioural synchrony (LM: $F_{1,252}$ = 18.756, p <.0001).

Table 4.2. Linear model outlining significant contributing variables to behavioural synchrony (log transformed).

Predictor Variables	Estimate	SE	F-test	P
Location			5.895	<.001
Inside	0.000	0.000		
Outside	-0.836	0.209		
Troop			4.131	<.001
West	0.000	0.000		
East	-0.2746	0.082		
Group Size	-0.021	0.018	18.496	<.0001
Group Size * Location	0.112	.024	21.671	<.0001

A full linear model identified a significant interaction between location and group size, where larger groups exhibited higher average levels of behavioural synchronisation when outside while the opposite effect was found when groups were inside (see Table 4.2 and Figure 4.2). This best model also identified significantly higher levels of behavioural synchrony in the West troop.

Figure 4.2. Linear regression lines representing the interaction between group size and location. Shaded lines represent the standard error of each regression line. Behavioural synchrony score in this graph has not been log transformed.
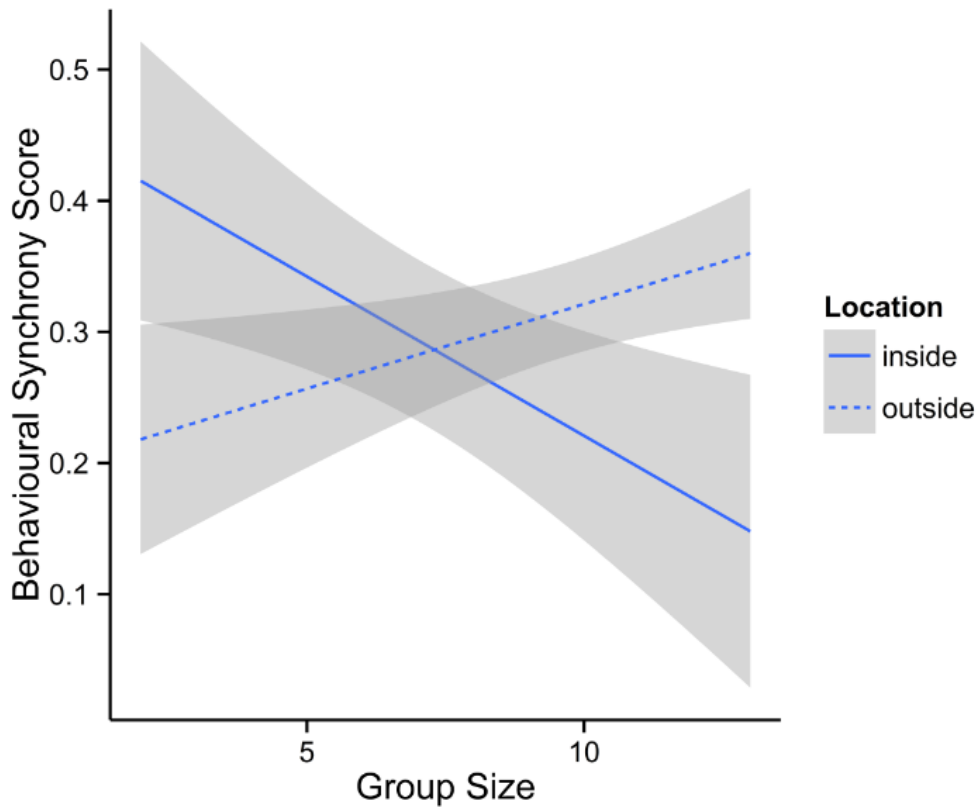
Vigilance and foraging were the only behaviours whose frequency in a scan was significantly correlated with behavioural synchrony (see Table 4.3).

Table 4.3: Correlation matrix examining relationships between the frequency of behaviours and behavioural synchrony; strongest positive correlations indicate behaviours that contributed the most to behavioural synchrony measures. Collinearity between behaviours were also examined. Kendall's tau statistic is presented with corresponding level of significance. BS = Behavioural Synchrony, F. Locomotion = Fast Locomotion.

	BS	Foraging	Vigilance	F.Loco-motion	Loco-motion	Rest	Groom
Play	.007 ns	.282***	-0.013 ns	-0.020 ns	0.041 ns	-0.109 ns	-.119*
Groom	-.037 ns	-.122*	0.047 ns	0.086 ns	-.018 ns	0.259***	---
Rest	.046 ns	-.078 ns	0.068 ns	-.096 ns	-0.014 ns	---	---
Locomotion	.002 ns	.122*	-0.028 ns	-0.040 ns	---	---	---
F. Locomotion	-.039 ns	-.038 ns	.090 ns	---	---	---	---
Vigilance	.261***	-.007 ns	---	---	---	---	---
Foraging	.093*	---	---	---	---	---	---

*p<.05, **p<.01, ***p<.001, ns >.05

Foraging behaviour was found to be positively correlated with locomotion and play (see Table 4.3), but negatively correlated with grooming. Also, grooming

behaviour was positively correlated with resting behaviour, and negatively correlated with play (see Table 4.3).

Social Facilitation

Examining environmental predictors of each behaviour using a GLM with logit link function identified vigilance behaviour as more common in the West troop. In addition, foraging behaviour was less likely to occur when raining and more likely to occur outside (see Table 4.4). Resting behaviour was also more likely to be observed in the West troop and was more likely to be observed later in the day (see Table 4.4). In the East troop, locomotion behaviour was more common and grooming behaviour was observed more often inside (see Table 4.4). Group size was a positive predictor of all behaviours in these models which is unsurprising given that the likelihood of any behaviour being observed during a scan increases in accordance with the number of individuals present.

Table 4.4: Logistic regression models examining what variables predicted whether a behaviour was performed during a scan. Dummy variables were created for this purpose so each dependent variable here is a binary variable (1 = present in a scan, 0 = not present during a scan).

Dependent Variable	Predictor Variable	Estimate	SE	Wald X²	P
Rest vigilant					
	Troop			7.212	.0072
	West	0.000	0.000		
	East	-0.492	0.147		
	Group size	0.342	0.039	108.767	<.0001
Foraging					
	Weather			6.566	.038
	Sun	0.000	0.000		
	Cloud	0.551	0.345		
	Rain	-1.642	0.895		
	Location			27.481	<.0001
	Inside	0.000	0.000		
	Outside	1.704	0.334		
	Group size	0.299	0.043	62.415	<.0001

Rest				
Troop			3.867	.0492
West	0.000	0.000		
East	-0.624	0.322		
Time	-0.114	0.058	3.896	.0484
Group size	0.2289	0.056	33.970	<.0001
Locomotion				
Troop			3.877	.0489
West	0.000	0.000		
East	0.517	0.264		
Group size	0.111	0.029	14.622	.0001
Groom				
Location			8.487	.0035
Inside	0.000	0.000		
Outside	-1.399	0.482		
Group size	0.211	0.065	12.875	.0003
Play				
Group size	0.305	0.062	40.749	.0001

To examine the effect of group size in a more valid way, the proportion of monkeys performing each category of behaviour was compared based on quartile measurements of group size. Group size was found to have a significant influence on the proportion of vigilance (GLM: X^2_3 = 212.70, p

<.0001), foraging (X_3^2 = 936.56, p <.0001), locomotion (X_3^2 = 589.05, p <.0001), resting (X_3^2 = 452.10, p <.0001), play (X_3^2 = 84.03, p <.0001), and grooming (X_3^2 = 153.84, p <.0001). A multiple comparison's test with Shaffer corrections is reported for consecutive quartiles in Table 4.5.

The proportion of monkeys exhibiting evidence of vigilance increased from the first quartile (mean = 0.262, SE = .036) to the second quartile (mean = .318, SE = .032), and also increased between the second quartile and the third quartile (mean = .352, SE = .032), but a significant decrease in vigilance was observed between the third and fourth quartile (mean = .268, SE = .027). The proportion of monkeys foraging increased over each consecutive quartile (1st quartile: mean = 0.079, SE = .026; 2nd quartile: mean= 0.123, SE = .022; 3rd quartile: mean = .209, SE = .033; 4th quartile: mean = .264, SE = .027). Locomotion, on the other hand, decreased over the first three quartiles (1st: mean = .300, SE = .041; 2nd: mean = .206, SE = .022; 3rd: mean = .163, SE = .020), and increased significantly in the final quartile (mean = .240, SD = .020). The proportion of monkeys resting significantly increased between the first (mean = .040, SE = .020) and second quartile (mean = .054, SE = .016), between the second and third quartile (mean = .142, SE = .031), and significantly decreased between the third and fourth quartile (mean = .059, SE = .016).

Table 4.5: Following the identification of a significant effect of group size multiple comparison tests were made to examine significant differences between consecutive quartiles. Model estimates from the GLM are reported with standard errors in parentheses; baseline comparison is always the lower quartile. P-values of comparisons are indicated by symbols.

	Quartile Comparisons		
	$1^{st} - 2^{nd}$	$2^{nd} - 3^{rd}$	$3^{rd} - 4^{th}$
Vigilance	0.194 (.033)***	0.100 (.031)**	-0.269 (.033)***
Foraging	0.444 (.056)***	0.531 (.046)***	0.234 (.038)***
Locomotion	-0.369 (.035)***	-0.244 (.043)***	0.394 (0.042)***
Rest	0.286 (.081)***	0.966(.063)***	-0.897 (.062)***
Play	0.538 (.094)***	0.016 (.084)ns	0.294 (0.079)***
Groom	-0.075(.108)ns	-0.613(0.140)***	-0.655(.186)***

*p<.05, **p<.01, ***p<.001, ns >.05

The proportion of play behaviour increased between the first quartile (mean = .027, SE = .019) and second quartile (mean = .047, SE = .013), there was no difference between the second and third quartiles (mean = .048, SE = .013), and proportion of play significantly increased in the final quartile (mean = .064, SE =

.014). There was no difference found in the proportion of grooming observed in smallest groups (mean = .027, SE = .017), and the second quartile (mean = .025, SE = .009), but the proportion of individuals grooming significantly decreased over the third and fourth group-size quartiles (3rd quartile: mean = .014, SD = .037, 4th quartile: mean = .007, SE = .027).

Between groups neighbour effects

For each behaviour, the correlation between the proportion of monkeys performing that behaviour in the East troop and the proportion of monkeys performing that behaviour in the West group was examined. When time of day, temperature, and group size are partialled out of correlations a positive relationship was identified between the proportion of vigilant monkeys in the east and west troops (see Table 4.6). Similar relationships were identified for play behaviour, fast locomotion, and resting behaviours (see Table 4.6).

Table 4.6: Spearman correlation coefficients for proportion of behaviours exhibited from both East and West groups, including the correlation coefficients once other possible confounds are partialled out of the analyses (temperature, time of day, and group size).

	Vigil-ance	Forage	Rest	Loco-motion	Feeding	F. loco-motion	Groom	Play
Spearman's Rho partialling out time, temp, and group size	.228*	.166	.314**	.029	.235*	.388***	.132	.292**
P value	.042	.144	.004	.801	.036	<.001	.250	.008

*=p<.05, **=p<.01, ***=p<.001

Discussion

The degree of behavioural synchrony identified in two groups of captive capuchin monkeys was significantly greater than expected based on a randomly generated dataset with individuals behaving independently. To my knowledge, this is the first evidence of behavioural synchrony at the group level in New World primates and in a captive population. Contrary to prediction one, examination of predictors of behavioural synchrony revealed that groups in their indoor enclosure exhibited decreased levels of synchrony. This finding is incompatible with previous findings that discovered increased

spatial proximity afforded greater opportunities to co-ordinate behaviour. However, on considering the interaction between location and group-size this effect is understandable. When outside, larger groups were found to have higher levels of behavioural synchrony (Figure 4.2). As the number of individuals in an enclosure increases, the average distance from a conspecific decreases, potentially creating more opportunities for social influence. But why wasn't this effect also observed in the indoor enclosure where the same basic principle applies? This effect might be attributed to a combination of increased heterogeneity in terms of hierarchical composition in large groups and the enclosed nature of the indoor space. Monkeys of varying social status might interpret a social environment in very different terms, especially when that environment is enclosed. Higher ranking individuals may interpret an enclosed indoor environment as safer and preferentially treat this area as a place to rest. However, the perceived threat of violence from a dominant aggressor may increase vigilance and locomotion in more subordinate monkeys. This increase in intra-group behavioural variability may be less relevant when outdoors as subordinate monkeys especially can decide to keep a greater distance from the dominant monkeys, pre-empting possible negative reaction. There could be other reasons for this interaction; however, further studies will be able to shed light on how individual differences contribute to variation in behavioural synchrony in different contexts. It is important to consider the possibility that an environmental cue, especially a social cue, will be interpreted and acted

upon in different ways by different individuals which will generate behavioural diversity within a group.

While it was predicted that smaller groups would exhibit greater behavioural synchrony, this effect was only noted when monkeys were inside (prediction 2; see Figure 4.1). The observation that behavioural synchrony increased with group size in outdoor enclosures could be attributed to a number of factors (see Table 4.2, and Figure 4.2). An increase in the number of conspecifics in this larger outdoor area may promote synchrony by increasing the likelihood that a groupmate will observe a conspecific's behaviour, thus facilitating any variety of social learning mechanisms (enhancement or contagion effects; see Chapter One for detailed descriptions of each). After all, perception of a social cue is necessary for an individual to be influenced by it. Whether the mechanism directly leading to an influencing effect is social contagion, or social facilitation, cannot be determined from the current data, however, future research should determine which mechanisms might determine behavioural synchrony at the level of the individual. For example, group-size effects may contribute to synchrony, as some behaviours measured here were found to be related with both behavioural synchrony and group-size (i.e. foraging, and vigilance behaviours).

Support was found for the third prediction that group size would positively influence vigilance behaviours, although the proportion of monkeys displaying vigilance behaviours did reduce in the largest groups. While this finding contradicts research on the effect of group-size on vigilance in other species of mammals and birds (Ebensperger et al., 2006; Lazarus, 1978; Pays et al., 2009), it complements research with primates (Hirsch, 2002; Treves, 1998, 1999) and corvids (Robinette & Ha, 2001). Hirsch (2002) has suggested that the heightened vigilance exhibited in larger groups of capuchin monkeys is due to pressure of monitoring conspecifics. While capuchin monkeys are notably tolerant of conspecifics (e.g. Ottoni, De Resende, & Izar, 2005), these monkeys inhabit a complex hierarchical group system (Fragaszy, Visalberghi, & Fedigan, 2004), and must be attentive to the behaviour of others. Some theorists have argued that certain forms of complex intelligence found in ape species are absent in monkeys (i.e. imitation, Fragaszy, Deputte, Cooper, Colbert-White, & Hémery, 2011; or self-recognition, Mitchell & Anderson, 1993). However, others have suggested that the intelligent processes facilitated by the large brains of monkeys might be related to processing social signals in a complex social space and reacting quickly, and correctly in accordance with their own immediate goals (Barrett et al., 2007). This proposed form of monkey-intelligence replaces the anthropocentric view of a Cartesian primate mind with a mind grounded in perception and action (Barrett et al., 2007). For example, a mind that may need to be extra vigilant in a crowded social space. Captive populations are also

unlikely to be as concerned with predator detection as wild animals, and without this factor driving vigilance levels in smaller groups, the effect of group-size on vigilance may be more pronounced.

The proportion of monkeys performing foraging behaviour significantly increased relative to group size across each quartile of group-size (prediction four). This finding corresponds with previous research on capuchin monkeys that found the presence of a conspecific facilitated successful foraging (Dindo et al., 2009b). However, this is the first study to demonstrate a positive relationship between group size and foraging behaviour in capuchins. While other studies of group-size in mammals and birds have discovered that larger groups facilitate foraging (Ebensperger et al., 2006), and the style of foraging behaviour (Beauchamp, 2013), this is the first report of a similar effect in capuchin monkeys. While in other studies, group foraging results in a reduction in vigilance (Ebensperger et al., 2006), this was not found in our analysis which produced no evidence of a significant relationship between the frequency of vigilance behaviour and foraging behaviour (see Table 4.3). This may be because increased vigilance relative to group size seems to be a unique characteristic of some primates (and some other species; e.g. crows Robinette & Ha, 2001). The proportion of play behaviour observed in our sample was significantly lower in the smallest groups, stayed constant over medium-to-

large groups, but was highest in the largest groups. Interestingly, the frequency of play behaviour positively correlated with foraging behaviour. It may be that this relationship is representative of differences between age or sex categories in our samples, with younger male monkeys more likely to be found playing, while females and older monkeys forage more. While these factors did not come within the scope of this study, future studies should investigate the individual differences that may interact with group-size effects. It is posited that the same mechanism that facilitates relaxed foraging behaviour in older monkeys may influence similar attitudes in younger monkeys which are displayed through different behavioural expression. Emotional contagion may also be the underlying mechanism behind socially facilitated play behaviour as has been posited in other social animals (Osvath & Sima, 2014). Resting was also found to be positively influenced by group size, again, potentially due to the tendency of monkeys to sleep in larger groups, especially near the end of the day. Finally, locomoting behaviour was more likely to occur when monkeys were present in smaller groups. It could be that when alone, or with only a small group of other monkeys, there is an increased necessity to patrol an enclosure for possible threats, both of a social and predatory nature. Also, it is important to remember that the capuchin monkeys studied here share their enclosures with squirrel monkeys, whose presence and behaviour are likely to influence some of the social effects examined here. For example, it is thought that one benefit of mixed-species groups is that vigilance can be shared

between individuals of different species without suffering some of the costs of large single species groups (e.g. mate competition; Wolters & Zuberbühler, 2013). Here, a first step was taken in exploring the effects of social influence within-species but future studies are necessary to tease apart the more complex nature of these effects in mixed-species groups.

Finally, this study examined neighbour effects between the two separate troops of capuchin monkeys. When other variables are partialled out of correlations, play behaviour and resting behaviour were positively correlated between East and West groups. However, this effect was not found for grooming behaviours. The inconspicuousness of grooming behaviour may have contributed to this finding. While monkeys resting on horizontal branches can easily be observed from an adjacent enclosure, and the vocalisations produced during play are similarly conspicuous, grooming behaviour is more discrete and less obviously visible from a distance. This provides partial support for our fifth hypothesis that affiliative behaviours may be related between groups. Similarly, while no direct measures of aggression were taken, we found partial support of our sixth prediction that unease would be correlated between groups, with evidence of correlated vigilance and fast locomotion between groups.

As the methodology employed in this study is an indirect test of the neighbour effect it is difficult to confirm that the correlations observed were definitively due to between-group social influence. Monkeys in some cases may have been influenced by other factors, including visitor effects that were not measured during this study (Hosey, 2000). These findings of correlated behaviours between groups of captive animals, complement evidence of neighbour effect in apes and other New World primates (Videan et al., 2005; Watson & Caldwell, 2010). Overall, these effects are under-examined in the primate literature and there are important reasons to encourage further research on this topic. Watson et al. (2014) induced a culture of increased affiliative behaviours by simulating neighbouring affiliative vocalisation, providing evidence that the manipulation of neighbour effects may improve captive welfare. Evidence of neighbour effects of aggression suggest that eavesdropping on distressed or aggressive neighbours may have a negative impact on group behaviours (Videan et al., 2005). This knowledge can provide guidance for the introduction of welfare measures; for example, reducing between-group contact when one group may have to undertake a potentially stress-inducing husbandry procedure.

This chapter has summarised and examined some of the phenomena that take place among group living primates. The literature on social learning often ignores the study of group level effects to the detriment of a complete

understanding of the social interaction. Theoretical and empirical steps have been taken to address this imbalance (Galef, 2013; King & Cowlishaw, 2009), and here a further attempt has been made. It is suggested that simultaneous observations of neighbouring groups should be used to understand the complex interactions between captive groups that may have auditory, visual, and even olfactory contact. Next steps should examine these effects on an inter-species level and specifically address the impact of these neighbour effects on captive animal welfare.

The study of social influence at the group level must be complemented with an examination of the mechanisms acting at the individual level that mediate behavioural responses. In many cases, the mechanisms of interest will not require complex cognitive processing, but understanding them is no less important. The mechanism of behavioural co-ordination or synchrony is enacted on the level of the individual, but the study of an interaction between group-level effects and individual effects introduces exciting possibilities for future avenues of research. In the next chapter, an experimental study will examine one potential mediator of group-level behavioural synchrony on the individual level. While the focus of this chapter has been group-level behavioural dynamics, the next will focus on changes in emotional state that

may mediate the relationship between contagious or synchronous behavioural

effects.

Chapter 5: Social contagion in capuchin monkeys

As discussed in the introduction, the study of cognitive mechanisms underlying social learning and social influence, especially in primates, has long been at risk of becoming side-tracked by focussing on mechanisms considered "complex". For conceptual reasons it might be useful to rank cognitive mechanisms in order of complexity (e.g. de Waal, 2008; Whiten & Ham, 1992), but arguing that certain processes are more worthy of empirical consideration is inimical to a complete understanding of social learning. For example, empathy, the process of adopting the emotional state of another, is defined at varying levels of complexity (de Waal, 2008). de Waal (2008) describes a nested model of empathy with emotional contagion (i.e. the automatic matching of another's emotional state) facilitating more complex empathic processes like perspective taking and empathic concern. But, to understand a hierarchical model of this type it is important that each component is understood in its own right. One group of mechanisms that may contribute to complex cognitive processes are categorised broadly as social contagion effects. Social contagion is defined as the "spread of affect, attitude, or behaviour from individual A (the initiator) to individual B (the recipient), where the recipient does not perceive an intentional influence attempt on the part of the initiator'' (p 266, Levy & Nail, 1993). While considered less cognitively taxing than true-imitation

(Whiten, 2000) or true-empathy (de Waal, 2008), these processes likely account for many examples of emotional and behavioural state-matching in human and nonhuman animals, and so are important to understand.

While the study of empathy is rarely examined explicitly in the social learning literature, it is often considered a related phenomenon. Indeed, some recognise it as an emotional equivalent of imitation based on evidence that both phenomena may be facilitated by mirror neurons (Iacoboni, 2009). Furthermore, simpler cognitive processes likely recruited in true-empathy (e.g. emotional contagion; de Waal, 2008), are sometimes explored in the social learning literature under the category of social contagion (see definition above). An individual possessing the capacity for true-empathy or cognitive-empathy must go beyond matching the emotional state of another, and cognitively distinguish another's emotion from their own, as well as act compassionately towards that individual (de Waal, 2008; Decety & Meyer, 2008; Hatfield, Rapson, & Le, 2009). From their second year human children have been found to possess the ability to differentiate between their own emotional states and those of others (Repacholi & Gopnik, 1997), and they also make efforts to alleviate the distress of others (Zahn-Waxler & Radke-Yarrow, 1990). Unexpectedly, each cognitive component of "true empathy" is also found in adults (for review see Decety, Norman, Berntson, & Cacioppo, 2012). However, evidence of the cognitive

processes necessary for true empathy in nonhuman animals is less apparent.

Chimpanzees, ravens, and elephants have been found to console distressed

conspecifics (Fraser & Bugnyar, 2010; Fraser, Stahl, & Aureli, 2008; Plotnik & de

Waal, 2014). Indeed, evidence of pro-social behaviour in rats directed towards

distressed conspecifics has also been presented as evidence of empathy (Ben-

Ami Bartal, Decety, & Mason, 2011). However, observing a distressed

conspecific may elicit a similar emotional response in an observer through

emotional contagion, and to quell one's own discomfort an observer may help

or console a conspecific. Due to the inherent difficulty in inferring goals of

empathic concern in animals, some have argued that no concrete example of

true empathic ability in nonhuman animals exists (Vasconcelos, Hollis,

Nowbahari, & Kacelnik, 2012).

Even evidence of the comparatively simpler process of emotional contagion is

difficult to identify. To overcome the problem of judging emotional contagion

from behaviour alone, physiological indicators of emotional arousal can be

examined following observation of an emotionally valenced social stimulus (i.e.

a conspecific's emotional expression). In humans, a number of studies have

shown that after watching an individual express distress, anxiety, or disgust, a

human observer produces a physiological response that matches the observed

emotional state (Buchanan et al., 2012; Waters et al., 2014; Wicker et al., 2003).

For example, the stress experienced from speaking in public elicits a similar stress response in individuals watching someone give a talk (Buchanan et al., 2012). Buchanan and colleagues found that the stress hormone levels taken from individuals watching anxious individuals giving a presentation increased in proportion to the stress hormone levels measured in the speakers. Second-order emotional contagion has also been identified in humans. Participants watching the face of another individual, who is watching a video of an actor producing joyful or fearful expressions, respond with facial expressions that correspond to the emotions portrayed by the actor (Dezecache et al., 2013**).** In animals, the best evidence of emotional contagion identified through physiological means is found during mother-infant interactions. For example, an infant chick's distress has been noted to induce a similar emotional reaction in the mother hens (Edgar, Lowe, Paul, & Nicol, 2011; using a similar procedure in non-related pairs of hens found no emotional contagion effect, Edgar, Paul, Harris, Penturn, & Nicol, 2012). One study of chimpanzees examined physiological correlates of emotion to identify emotional contagion. Following presentation of video footage showing a conspecific being injected with a needle and syringe, chimpanzees experienced a reduction in peripheral skin temperature indicative of physiological arousal (Parr, 2001). However, a similar physiological response was identified when chimpanzees were observing videos of needles without a conspecific present, so it is unclear if the physiological reaction was elicited by the emotional reaction of a conspecific

(i.e. evidence of emotional contagion) or because of a potentially threatening stimulus. A more recent video playback experiment found that chimpanzees watching videos of conspecifics performing a range of emotionally valenced behaviours (e.g. aggressive interactions, infanticide), showed no congruent emotional response to the videos (however, emotion in this case was measured behaviourally; von Rohr, van Schaik, Kissling, & Burkart, 2015).

Overall, evidence of emotional contagion measured through physiology is rare in animals and in most cases, evidence of emotional contagion has been provided from behavioural data. However, acknowledging that behaviour is our primary source of information about an animal's goals, emotional state, and preferences, it is important to recognise the difficulty in teasing apart emotional contagion from response facilitation or behavioural contagion. We know that a number of behaviours are related to underlying emotional state. However, if we find that these behaviours are being socially facilitated, is it possible to conclude that emotional state is also being transmitted (see Chapter Six for a more detailed discussion)? While it is difficult to differentiate between emotional and behavioural contagion, one recent study found that ravens were more likely to adopt a playful mood (i.e. a motivation to perform one of a number of play behaviours) after seeing a conspecific playing (Osvath & Sima, 2014). This example is particularly convincing as the play behaviours exhibited

by the observer ravens did not necessarily involve the same actions they had observed, rather an action belonging to a class of behaviours associated with play. The most convincing evidence of emotional contagion in primates is similar; i.e. an individual is exposed to an emotionally valenced stimulus and reacts with behaviour that suggests a change in affective state has taken place. For example, the neighbour effect that was examined in the previous chapter is sometimes credited as evidence of emotional contagion. Baker and Aureli (1996) found that when aggressive calls were made by neighbouring groups of chimpanzees, the focal group would also be more likely to perform aggressive actions (not necessarily aggressive vocalisation). A more recent study found that affiliative behaviours were similarly affected by neighbouring group vocalisations (Videan et al., 2005). Common marmosets (*Callithrix jacchus*) were also found to show increased levels of affiliative behaviours when vocalisations from a neighbouring captive group were affiliative, and the opposite effect was observed when neighbouring groups produced negative or aggressive calls (Watson & Caldwell, 2010). Under experimental conditions it was discovered that an increase in affiliative behaviours could be induced through playback of affiliative vocalisations, suggestive of emotional contagion (Watson, Buchanan-Smith, & Caldwell, 2014). Together, these results demonstrate a form of social influence indicative of emotional contagion, however, without more controlled study it is difficult to specifically identify whether emotional state matching is crucial for these effects to occur.

In humans, it has been suggested that facial mimicry is indicative of emotional contagion as variation in physiological responses associated with emotional arousal (i.e. skin conductance variation) correlate with facial mimicry (Dezecache et al., 2013). Facial mimicry may then be the best evidence of emotional contagion found in nonhuman primates, and has been identified in orangutans (P*ongo pygmaeus*, Ross, Menzler, & Zimmermann, 2008), chimpanzees (*Pan trogladytes*, Davila-Ross, Allcock, Thomas, & Bard, 2011) and baboons (Mancini, Ferrari, & Palagi, 2013). Behavioural evidence of emotional contagion in humans is found in infants crying to the sound of other babies crying but not in response to other stimuli of a similar intensity (Martin & Clark, 1982). Humans rapidly match facial gestures that communicate affective states (e.g. Bourgeois & Hess, 2008; Hess & Blairy, 2001), and there is some evidence that creating facial gestures linked to emotion can cause a subject to exhibit autonomic responses indicative of emotional arousal (Ekman, Levenson, & Friesen, 1983). It may be then that rapid facial mimicry may help mediate emotional contagion rather than act as an observable behavioural response of an underlying emotional effect. However, while facial mimicry may be indicative of emotional contagion, it has yet to be identified in non-play interactions, so it may be that this phenomenon is specific to these interactions and is communicative rather than contagious. Also, further work is necessary to show that the underlying emotions being experienced are indeed congruent

170

rather than complementary, and are not triggered by other environmental stimuli that may cue play behaviour.

While studies of emotional contagion are not common, examples of behavioural synchronisation are more prevalent in the nonhuman literature. The ability to detect and react according to the behavioural states of conspecifics is adaptive, and many species use the behaviours of conspecifics to cue their own. The synchronous movement governed by simple heuristics witnessed in flocks, swarms, herds, schools, and other large groupings of animals provide convincing evidence that cognitive intelligence is not necessary to coordinate group behaviour (Beauchamp, 2012; Couzin et al., 2002; Reynolds, 1987). This coordinated movement is important for adaptive group living, and aids in predator detection and avoidance (Beauchamp, 2009; Carere et al., 2009; Ebensperger et al., 2006). Sometimes however, the function of co-ordinated behaviour is less obvious. One area that has received considerable interest is the study of socially facilitated displacement behaviours. Displacement behaviours are a class of behaviour defined by their apparent irrelevance to the situation in which they occur. They are often related to body care (e.g. self-grooming, self-scratching, yawning, body-shaking, preening, etc.), but also occur during instances of stress, thwarting, or indecision (Delius, 1967; Diezinger & Anderson, 1986; Maestripieri, Shino, Aureli, & Troisi, 1992; Sevenster, 1961).

Curiously, many displacement behaviours appear to be socially facilitated. The most common example is that of yawning, however, there is evidence that scratching in primates (Feneran et al., 2013; Holle et al., 2012), and preening in birds (Hoppitt et al., 2007; Palestis & Burger, 1998), are also socially facilitated. As displacement behaviours are linked with emotional arousal it is difficult to differentiate between emotional and behavioural social transfer in these instances. Is socially contagious preening or scratching indicative of a change in emotional arousal, or merely coordinated body-care behaviour? This study will attempt to address the difficulty in interpreting emotion from behaviour, and Chapter Six will address in detail the issue of contagious displacement behaviour.

To examine in greater detail the transmission of behavioural and emotional states we attempted to examine these effects under experimental conditions in capuchin monkeys (*Sapajus sp.*). As mentioned in Chapter 1, capuchin monkeys are a socially tolerant group-living species that are well known for their large brain to body size ratio (Fragaszy et al., 2004), and a number of studies have examined the ability of capuchin monkeys to learn from others with mixed results (Dindo et al., 2009b; Fragaszy et al., 2011). Capuchin monkeys can learn about the edibility of food from conspecifics (Visalberghi & Addessi, 2001), foraging behaviour is enhanced through the presence of conspecifics (Dindo,

Whiten, & de Waal, 2009), and in a two-action task, different methods of opening a puzzle box (either lifting a window upward, or sliding it to one side) were reliably copied (attributed to emulation; Dindo, Thierry, & Whiten, 2008). However, evidence of more complex imitation is lacking. Little support for the possibility of capuchins learning complex tasks purely from observing a conspecific has been found (for a review see Visalberghi & Fragaszy, 2001), and behaviour matching is limited to actions that require the manipulation of an object (Fragaszy et al., 2011). Interestingly, while capuchin monkeys have been the focus of numerous studies of social learning, no study has yet examined emotional or behavioural contagion with this species.

In this current study, we presented monkeys with video stimuli representing conspecifics from their group in a number of emotionally valenced scenarios (e.g. monkeys displaying threat displays, grooming each other, foraging), to examine whether an emotionally contiguous response would be elicited by the observer monkeys. To rule out the possibility of a stressful stimulus generating an emotional response, rather than the emotional reaction of the conspecific, the video stimuli presented in this study never displayed the stimulus that was eliciting the reaction in the monkeys in the video. Many studies of emotional contagion have only measured the behaviour of an observer (e.g. Davila-Ross et al., 2008; Osvath & Sima, 2014), but both behaviour and physiology were

measured here. By examining both the behavioural response of the observer monkeys as well as stress hormone levels measured through salivary cortisol, it was possible to examine contagion both behaviourally and physiologically. Levels of cortisol, a steroid hormone released through the adrenal cortex, measured in the blood, urine, or saliva has been used to assess stress levels in primates for a number of years (Heintz, Santymire, Parr, & Lonsdorf, 2011; Tse & Bond, 2004). Cortisol levels increase in response to psychological and physiological stressors, (for review see Dickerson & Kemeny, 2004), and the release of cortisol into the blood can be measured in saliva within one minute (Vining, McGinley, Maksvytis, & Ho, 1983). However, unlike blood or urine sampling methods, saliva can be collected non-invasively at multiple time-points separated by short intervals.

Our primary hypotheses concern social contagion in capuchin monkeys. However, as this is the first study to examine salivary cortisol in capuchin monkeys, a secondary aim was to examine variance in the cortisol measured. Cortisol has been found to follow a daily circadian rhythm in some primates peaking in the morning and dropping throughout the day (Chan & Debono, 2010; Heintz et al., 2011), and as research sessions took place at two different time points in the day, it was possible to examine this daily variation for the first time in capuchin salivary cortisol. Also, the collection of salivary cortisol

allowed an assessment of average variation of cortisol in primates throughout a research session. An important consideration when conducting research with captive animals is the assessment and improvement of subject welfare for both ethical and empirical reasons (Ash, 2014). The sampling of salivary cortisol allowed an examination of whether the monkeys became increasingly stressed due to their voluntary separation from their social group.

This study's primary aim was to examine the change in both behavioural and emotional responses as a result of social stimuli. It was predicted that measures of anxiety and cortisol would be greatest during stimuli containing video representations of anxious group-mates in comparison to social control videos (i.e. stimuli showing neutral behaviours, e.g. feeding, foraging), and non-social control videos containing recordings of enclosures without monkeys present. If emotional contagion mediates transmission of affiliation and a sense of ease, it is expected that observation of videos containing groupmates in more relaxed scenarios (i.e. resting or grooming) might reduce stress hormone levels as well as stress related behaviours in comparison to control stimuli. Furthermore, while the behaviours used to assess emotion are presumed to correlate with stress responses based on previous research of displacement behaviours linked to stress (for a review see Maestripieri, Schino, Aureli, & Troisi, 1992), this study was also able to assess the validity of behavioural measures as indicators

of arousal, measured here through cortisol. Behaviour was examined in the context of a change in cortisol over a research session and average cortisol over a session. An average measure of cortisol is likely indicative of the monkey's general state of arousal at the time of the session and will vary across sessions dependent on the monkey's experience both during the research session and before the session. On the other hand, examining a measure of change in cortisol informs us of behaviours that might be more indicative of a real-time change in arousal.

Methods

Animals and research site

Research was conducted at the Living Links to Human Evolution Field Site at Edinburgh Zoo. For further information concerning layout, husbandry practices, and population make-up at this research site see Chapters Two and Four. As previously described in Chapter Two, research rooms situated between both East and West capuchin and squirrel monkey enclosures facilitate the study of monkeys in isolation or in smaller groups. For the purpose of this study ten capuchin monkeys (*Sapajus sp.*) were tested (eight males, mean age = 6.33 years; SD = 3.43), between 16.09.2013 and 09.12.2013. Experimental sessions took place twice daily, four times a week, and participation was rewarded with raisins, peanuts, and sunflower seeds. Diluted pineapple juice

was used for training, and all rewards were supplementary to the primates' diets. Ethical approval was granted for this study by the University of Stirling's Ethics Committee.

Materials

Eight research cubicles arranged in a connected 2X4 matrix act as a corridor between the monkeys' indoor and outdoor enclosures (each cubicle measures 49.5 cm X 52.1 cm X 51.4 cm). Partitioning slides inserted between cubicles allow monkeys to be separated from their groupmates for research purposes, and for this study subjects were granted access to two adjacent, middle cubicles (see Figure 1). Video stimuli were recorded using a Sony Mini Digital Video Camera, and video stimuli were presented using Microsoft PowerPoint on a 19" LCD monitor. Cotton swabs were used to collect saliva from monkeys at various stages of the research session (Salimetrics, SalivaBio Children's Swab).

Stimuli

At the time of the study dominant males from both East and West groups did not take part in research sessions, so these individuals were recorded for use in the video stimuli. In some stimuli videos, other monkeys were present in the video, but these monkeys were never subjects. Monkeys included in the stimuli

were observed in their enclosures and recorded on a digital video camera. Extracts of recorded video were chosen to represent a variety of different emotional states in capuchin monkeys. Neutral control stimuli included video recordings of the dominant male, alone or with other monkeys, sitting or moving in a relaxed state foraging or eating. Positive stimuli showed the dominant male grooming or being groomed by another monkey. Negative stimuli included the dominant male demonstrating stress related behaviours; e.g. performing a threat display, being highly vigilant. The monkeys in the video were never directly orientated towards the observer and while the monkeys in the stimuli may occasionally glance in the general direction of the camera lens, the video stimuli were designed to give the impression that the observed monkeys were being eavesdropped upon. Non-social control stimuli were also created. These included recordings of a section of the indoor and outdoor enclosures with no animal in view. As two groups of monkeys were tested in this study (i.e. East and West groups), two separate sets of group-specific stimuli were developed. For each group, two different stimuli were created for each of the emotionally valenced conditions (e.g. two positive stimuli videos for presentation to capuchins in the East group, and two different positive stimuli for the monkeys in the West group). Each stimulus was presented once during a morning research session and once during an afternoon research session to control for possible circadian variation in cortisol levels. In total, the design included the presentation of four stimulus types

(non-social control, neutral control, positively valenced, negatively valenced), each with two distinct video stimuli, each shown to the subject twice (in the morning and afternoon). Overall, each subject took part in 16 research sessions. However, one monkey (Inti) stopped taking part in research sessions at the end of this study and did not complete one session (data from the remaining 15 sessions was analysed). Data from 159 research sessions was analysed. Due to experimenter error, one monkey (Chico) was presented with the first positively valenced stimulus twice on consecutive morning research sessions. The stimulus was presented to this monkey a third time during an afternoon session (to counterbalance daily variation in cortisol) and these data were analysed instead.

Training for collection of saliva sample

Before the onset of the study monkeys were trained to chew on a cotton swab (Salimetrics, SalivaBio Children's Swab) by rewarding a series of approximate behaviours. At the first stage, monkeys were rewarded for any behaviour that increased the proximity between the swab and the monkey's face (often achieved when a monkey would try to smell the novel item). Subsequently, monkeys were rewarded for any further interaction with the swab involving their mouth (licking, sucking, biting, etc.). To discourage monkeys from touching the swab, if the swab was touched by the monkey's hand, the

experimenter would withdraw the swab and turn their back to the monkey signalling that approximately 5 seconds would elapse before the monkey would next get the opportunity to achieve a food reward. This method continued until each monkey would keep the swab in their mouth for a number of seconds. To encourage some monkeys to take the cotton swabs in their mouth, the swabs were first soaked in a pineapple juice and water solution (1:1 dilution). Once the monkeys had learned that they could suck on the swab to receive juice, the swab was offered dry. Once a monkey would take a swab in their mouth it was retracted and a food reward was offered. This was repeated until the swab looked visibly wet, which took approximately one-two minutes.

Before the experimental sessions began a saliva sample from each monkey was centrifuged (at 3600 rpm for 10 min) to assess whether sufficient saliva was being collected. Once it was clear that a monkey was providing sufficient saliva for analyses, monkeys were deemed ready for the experimental procedure.

Procedure

The monkeys at this research centre have been trained to signal their intent to end a research session by pushing against the cubicle doors that lead to their enclosures. Piloting the procedure with control non-social stimuli different to

180

those used experiment identified an optimal interval of five minutes between the onset of the first stimulus and the collection of the second sample of saliva. When longer time intervals were used, some monkeys persistently signalled to leave and sessions were terminated. Cortisol is transferred from the blood to saliva in approximately one minute (Vining et al., 1983), and the second saliva sample was expected to reflect the monkey's hormonal response to the video presentation. In humans, the effect of a stressor on salivary cortisol is most evident 20-40 minutes after the onset of the stressor, however, significant effects are identified after ≤10 minutes (Dickerson & Kemeny, 2004). During piloting, no noticeable change in stress-related behaviours (i.e. see definitions in Table 5.1) were identified throughout this five minute interval suggesting this time spent separated from their group was not stressful in itself. However, as this may be difficult to assess through behaviour alone, this effect was also examined as an aim of this study.

An experimental session began once a subject was separated from other monkeys and once all other monkeys had left the bank of research cubicles (i.e. not in any of the compartments seen in Figure 1). Once all entrances to the cubicles were closed, the experimenter took a baseline saliva sample from the subject. After this sample was successfully taken, a video monitor was placed approximately 50 cm from one of the two cubicles in use. The monkey was free

to stay in the experimental cubicle (i.e. the cubicle facing the video monitor) or move to the adjacent cubicle, however, food rewards were only offered in the experimental cubicle.

During each session the same 15 second video stimulus was presented to the monkey on four occasions. The presentation of the stimuli was automated using Microsoft Powerpoint. Each of the four stimulus presentations was preceded by a five second presentation of an olive green screen with a moving dot. The second stimulus presentation immediately followed the first and this was followed by a 15 second interval where the subject was offered a peanut half. The third and fourth presentation followed and after the final stimulus presentation the screen went black. Every fifteen seconds a beep sounded signalling the presentation of a single food reward (peanut half or sunflower seed). This continued for 3 minutes and 15 seconds when a different sound signalled for a second saliva sample to be taken. The soaked saliva swabs were immediately placed on ice packs and were placed in a freezer at -20°C within one hour. The interval between the first and second saliva sample was approximately 5 minutes ± 10 seconds.

During each session the subject's behaviour was recorded in both cubicles on a Logitech HD Webcam (C270). All videos were subsequently coded for

behaviours related to stress (see Table 5.1 for definitions). Vigilance and scratching behaviours were examined as well as the number of times the monkeys moved between the two cubicles (a proxy measure of activity). Monkeys are also trained to touch the doors leading to their enclosures as an indication that they would like to leave. Isolated door touching events during a session were measured as possible indicator of discomfort, whoever, if door touching behaviour persisted, a research session would be terminated and the monkey would be allowed to leave. This did not occur during the sessions in which the data was collected, however, some research sessions were terminated before baseline saliva samples were taken as monkeys gave clear indications of discomfort. Also, three other monkeys were trained to provide saliva samples but were not comfortable remaining in the cubicles for the required interval and did not complete more than five experimental sessions each. While the amount of time spent in the non-experimental cubicle could indicate an arbitrary preference, it may also indicate a preference to be further from the stimulus so this was also examined. Finally, attention paid to each stimulus was measured to examine any attentional preference.

Table 5.1: Definitions of behaviours used to examine emotional contagion in capuchin monkeys. Scratch, touch door, and peep were recorded as events. For a new event to be recorded the previous bout of behaviour must have terminated at least 5 seconds before the onset of the new bout.

Behaviour Name	Definition
Attention	The monkey's eyes are focussed in the direction of the monitor (i.e. just below the camera recording the behaviour).
Scratch	The nails of one of the monkey's hands or legs are moved across a part of the skin repeatedly. A new event was not coded if the location of the scratching moved.
Cross middle	The monkey leaves the focal cubicle to enter the second cubicle; both front and back legs must leave the experimental cubicle.
Touch Door	The monkey puts pressure on the outer slide indicating that he/she may want to leave. This may be a hand placed on the door with little pressure; or pushed with the monkey's entire body; sometimes the door is pulled by hand if there is a small opening, and the separating slide isn't flush with the back wall.
Vigilance	The monkey looks through the holes on the top or bottom of the separating slide or looks through the bottom slide.
Time in Second Cubicle	Time spent in second cubicle was measured in seconds.

Hormone analysis

The hormone analysis took place in the Endocrinology Lab of the Department of Behavioural Biology, University of Vienna, Austria. In order to keep the

samples frozen during transport from Edinburgh to Vienna, they were sent overnight on dry ice. The monkeys' saliva was gained by centrifuging the cotton swabs (3600 rpm, 10 min), and salivary cortisol concentrations were measured in duplicates, using an enzyme immunoassay (EIA) against Cortisol-3-CMO:BSA (for a detailed assay description see Palme & Möstl, 1997). This assay has already been used successfully in other species, including primates (i.e. bonobos, *Pan paniscus*, Behringer et al. 2009), horses (*Equus ferus caballus*, (Schmidt, Aurich, Möstl, Müller, & Aurich, 2010), and dogs (*Canis lupus familiaris*, Kotrschal, Schöberl, Bauer, Thibeaut, & Wedl, 2009). Intra and interassay coefficients of variation were 8.1 % and 10.8 %, respectively. Some samples were not analysed due to contamination or insufficient saliva leaving a total of 145 baseline samples (from 159 collected samples), 149 second samples, and 138 pairs of samples (i.e. available baseline and second samples from the same session). Overall, using the collection method described above, 92.5% of samples were able to be analysed, a rate comparable to other studies that have used similar methods with nonhuman primates (e.g. 88% success by Lutz, Tiefenbacher, Jorgensen, Meyer, & Novak, 2000).

Data Analysis

Daily and within-session variation in cortisol

To examine daily variation in cortisol levels the hour a saliva sample was taken (11:00- 12:00, 12:00-13:00, 14:00-15:00, and 15:00-16:00) was included as a predictor variable in a linear mixed model (LMM) with baseline cortisol levels as the outcome variable and subject included as a random factor. Baseline cortisol was log transformed to improve normality, but visualisations of this data and descriptive statistics represent non-transformed data. To test whether cortisol levels changed on average between the baseline measures and second measurement, a repeated measures Wilcoxon signed-ranks test was performed on the combined data to examine any group level effects. However, as multiple measures from each monkey were included in this group-level test, a series of repeated measures Wilcoxon signed ranks tests compared individual variation.

Effect of stimuli on behaviour and cortisol levels

One monkey was excluded from the examination of the effect of the emotionally valenced stimuli on behaviour and cortisol. Sylvie, had the highest mean levels of baseline cortisol (mean = 330.1 ng/ml) and also the highest variance (standard deviation, SD = 186.4 ng/ml; see Figure 2). Further examination of video from this individual's research sessions identified that

high mean and variance were likely unrelated to the experimental design and instead artefacts of separation from her infant. To examine the effect of stimulus type on stress hormone levels, an absolute change in cortisol over the research session was used as a dependent variable. This was calculated by subtracting the value of the cortisol measured in the baseline sample (taken before stimulus presentation) from the value of the cortisol measured in the second sample (taken approximately five minutes after the onset of the stimulus). Absolute change, rather than relative change, was used as a comparable absolute change in cortisol (e.g. 10 Ng/ml) can be vastly different in relative terms depending on the baseline measure (e.g. if baseline levels are 10 Ng/ml, a 10 Ng/ml change represents a 100% increase, while if a baseline measure of 100 Ng/ml is taken this change represents only a 10% change in cortisol). Behavioural outcome variables measured as continuous variables (attention, time in second cubicle) were examined for normality and non-normal data were transformed to improve the distribution of residuals in models (e.g. both attention and time in second cubicle were transformed using a logarithmic transformation). However, descriptive data and graphical representations of data are based on non-transformed values. Linear mixed-models were used to examine the effect of the stimulus type on the absolute change in cortisol, attention, and time spent in second cubicle. Poisson-distributed error structures are advised when handling count data (Zuur et al., 2009), however a comparison of model diagnostics from Poisson and Gaussian distributions identified no advantage to

Poisson models, so linear-mixed models are reported below. When necessary, count variables were transformed (log transformations) to improve error-structure (i.e. scratch, cross middle, touch door, and peep). As each monkey was tested multiple times on each condition, subject was always included in a mixed model as a random effect. The significance of stimulus type on outcome variables was assessed using F-tests. If significant effects were identified for the stimulus type, post-hoc comparisons explored the simple effects with adjusted p-values using the Shaffer method (Shaffer, 1986).

Behavioural Predictors of Cortisol

To examine behavioural predictors of cortisol, two linear mixed models were designed with subject as a random factor. One model examined behavioural predictors of an absolute change in cortisol between baseline levels and the second sample. Two outlying data-points (> 4 standard deviations from the mean) displayed very large residual values in the model (>4) and were removed from the final model. A second model examined behavioural predictors of average cortisol over the research session; the dependent variable in this case was the mean value of the baseline and second sample. A logarithmic transformation was performed on the average cortisol level to improve the fit of the linear model, and one data-point (>3 SD from the mean) was removed to improve model fit. As average cortisol was log transformed, to

describe the contribution of predictor variables, odds ratios were calculated through back-transformation of log odds. A backwards stepwise method was used to create each model. First, all independent variables were included in the models. Predictor variables were subsequently removed from each model in order of least significance. The final models with all significant contributing variables are reported. Variance inflation factors (VIF) were calculated for all predictor variables to test for collinearity and no evidence of collinearity was identified (all VIFs < 5, Zuur et al., 2009).

Software

All statistics test were performed using R statistical software (R Core Team, 2014) run in the Rstudio environment (RStudio, 2014). Linear mixed models were created using the lme4 package (Bates et al., 2015). All graphics were created using the ggplot package (Wickham, 2009).

Results

Variation in cortisol

There were considerable individual differences in monkeys' baseline average cortisol scores and variance (see Figure 5.1). A linear mixed model (LMM) found that the time of day had a significant effect on baseline cortisol levels ($F_{3,132} = 5.377$, p = .002).

Figure 5.1: Boxplot of baseline cortisol for each individual monkey. All boxplots display median values (solid horizontal lines) with inter-quartile ranges (upper and lower limits of the boxes), and maximum and minimum values within 1.5 times the inter-quartile range measure from the upper and lower hinges. Outliers are represented with filled dots and are values outside 1.5 times the inter-quartile range measured from both hinges.
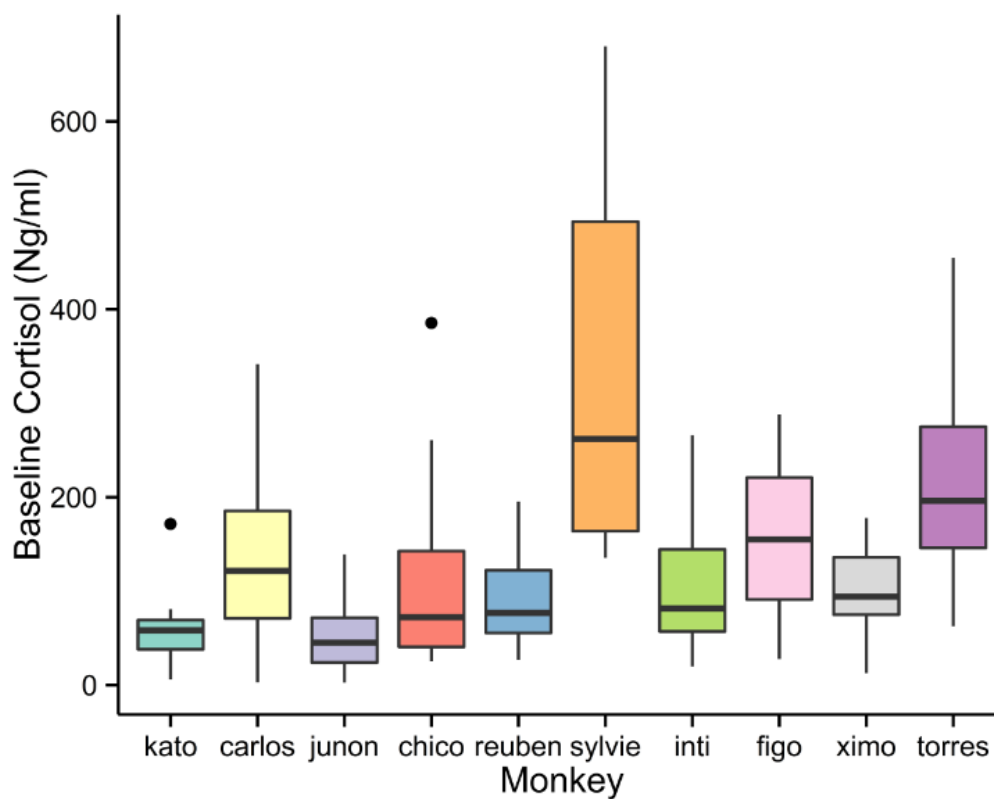
Post-hoc comparisons (with adjusted p-values - Shaffer methods) found that cortisol levels were higher between 11:00-12:00 (mean = 125.646 Ng/ml) than measures taken between 14:00-15:00 (mean = 109.260 Ng/ml) although this effect was only marginally significant (t = -2.133, p = .098). There was also a significant difference between cortisol levels measured between 11:00-12:00 and

those taken between 15:00-16:00 (mean = 124.6179 Ng/ml, t = -3.185, p = .007; see

Figure 5.2). Cortisol levels were also significantly higher when taken between

12:00-13:00 (mean = 187.733 Ng/ml) than when they were when taken between

15:00-16:00 (t = -3.243, p =.007; see Figure 5.2).

Figure 5.2. Boxplot representing baseline cortisol levels taken at different time-points in the day. For a description of boxplot components see Figure 5.1.
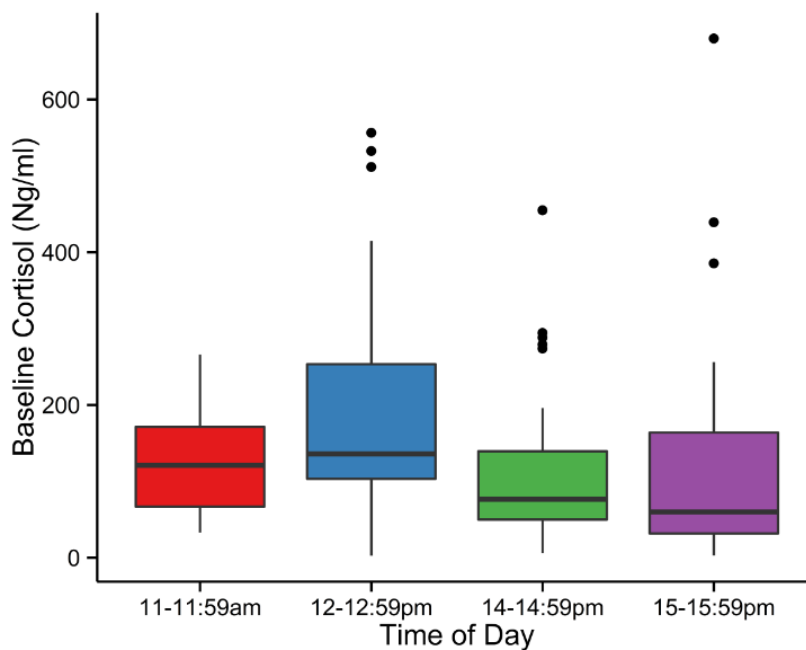
Overall, no significant difference was found between baseline measures of

cortisol (median = 104.4) and the second measures (median = 103.6; Wilcoxon

signed-ranks test: Z = - 0.896, p = .185). Examining the change in cortisol for

each individual monkey identified two monkeys whose cortisol levels

significantly changed throughout the sessions (see table 5.2).

Effect of stimuli on behaviour and cortisol levels

A linear mixed model (LMM) with individual monkey as a random factor, found that the type of stimulus had no effect on absolute change in cortisol (LMM: $F_{3,113}$= 0.141, p = .935; see Figure 5.3). Similarly, stimulus-type did not influence the amount of time the monkeys would spend in the second cubicle (LMM: $F_{3,131}$= 0.133, p =.941), frequency of movement (LMM: $F_{3,131}$ = 1.134, p = .338), door touches (LMM: $F_{3,131}$ = 1.047, p = .374), vigilance behaviours (LMM: $F_{3,131}$ = 0.432, p = .731), or scratches (LMM: $F_{3,131}$ = 0.234, p = .873).

Table 5.2. Median measures of cortisol at baseline and after the stimulus for each monkey. P-values and Z scores from Wilcoxon signed-ranks tests are also presented to test significant differences between baseline and seconds scores.

	Kato	Carlos	Junon	Chico	Reuben	Sylvie	Inti	Figo	Ximo	Torres
Median Baseline Cortisol (ng/ml)	58.25	121.55	45.1	72.2	76.8	261.85	81.5	155.1	94.2	196
Median After Cortisol (ng/ml)	45.1	116	80.55	63.3	98.3	237.65	94.05	101.2	108.1	201.3
Z (p-values)	0.667	-0.439	1.665	-.460	0.702	-0.105	0.785	-1.337	1.933	-.869
	(.252)	(.670)	(.048)	(.677)	(.241)	(.542)	(.216)	(.091)	(.027)	(.808)

A linear mixed model with individual as a random factor found that condition had a significant effect on attention to stimuli (LMM: $F_{3,131}$= 7.354, p < .0001; see Figure 5.4). Post-hoc comparisons (with adjusted p-values) found that significantly greater attention was paid to negatively valenced stimuli (mean = 11.45, SD = 8.57) when compared to neutral stimuli (mean = 8.12, SD = 6.93; t = - 2.296, p = .043), positive stimuli (mean = 7.13, SD = 8.12; t = -3.960, p = .0002), and control stimuli (mean = 6.15, SD = 6.70; t = -4.130, p = .0002). No other significant differences were found in attention to stimuli.

Figure 5.3. Boxplot of absolute change in cortisol for each condition. For a description of boxplot components see Figure 5.1.
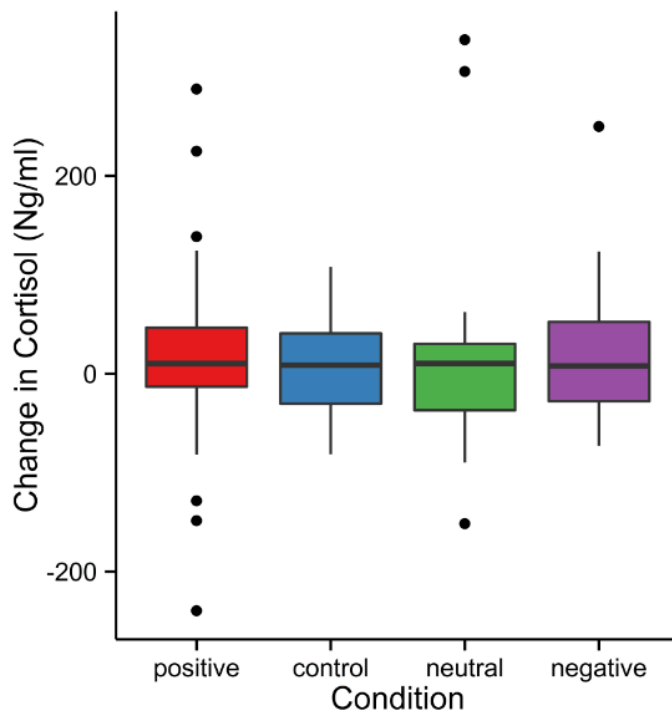
Figure 5.4. Boxplot of attention to videos for each condition. For a description of boxplot components see Figure 5.1.
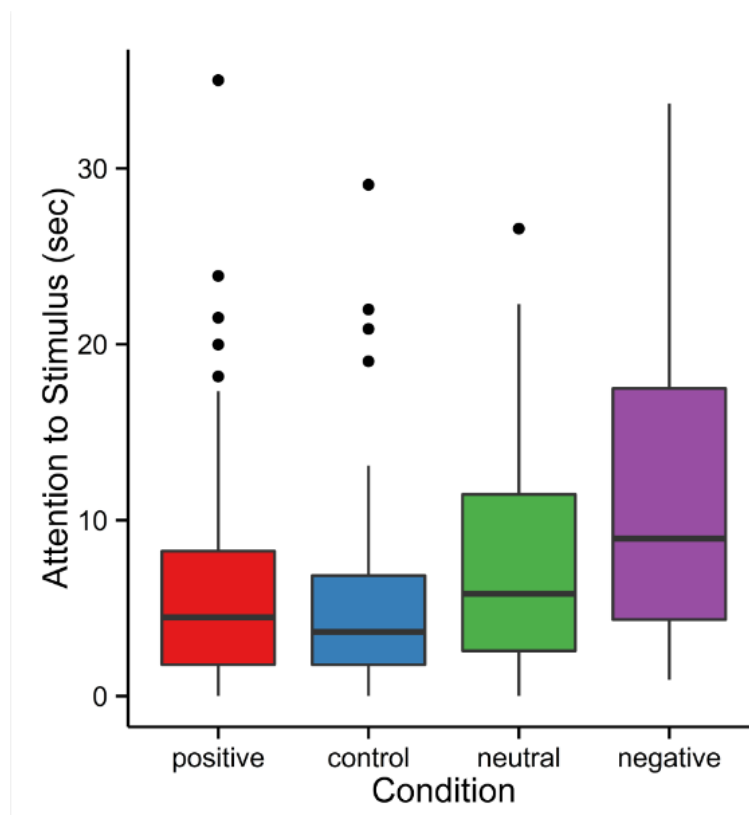
Behavioural predictors of cortisol

An LMM identified that the frequency of vigilance behaviours was a significant predictor of absolute change in cortisol over 5 minutes with an average decrease of 12.05 ng/ml of cortisol for every unit increase in vigilance behaviour (see Table 5.3.). One indices of discomfort was found to be marginally significant in predicting change in cortisol, with an observed increase of 12.66 ng/ml on average for every one observation of a monkey pushing against the research cubicle door (see Table 5.3.).

Table 5.3. LMM describing change in cortisol over 5 minutes (DV = absolute change in cortisol), and average cortisol in a research session (DV = sum of baseline cortisol values and second values).

Dependent Variable	Predictor Variables	Estimate	SE	T	P
Absolute Change in Cortisol					
	Constant	28.472	13.377	2.13	.0353
	Vigilance	-12.048	4.284	-2.81	.0057
	Push door	12.660	6.671	1.90	.0601
Average Cortisol					
(log transformed)					
	Constant	5.115	0.197	25.85	.0001
	Attention	-.0286	0.009	-3.02	.0031
	Vigilance	-.0707	0.034	-2.20	.0381
	Scratch	-.0775	0.042	-1.84	.0678

Examining average cortisol it was identified that attention and vigilance significantly predicted average cortisol levels; a unit increase in attention predicted an average reduction of 2.82% in average cortisol, while a unit

increase in vigilance predicted a 6.83% reduction in average cortisol (see Table 5.3). A marginally significant effect of scratching was identified with a unit increase in scratching predicting a 7.46% reduction in average cortisol (on average).

Discussion

An attempt to study emotional contagion in capuchin monkeys discovered that the type of emotionally valenced stimuli presented to subjects did not systematically affect any behaviours related to emotion or arousal (i.e. scratching, comfort in the research cubicle, vigilance), or physiological stress responses measured through salivary cortisol. However, monkeys did attend significantly longer to stimuli depicting conspecifics demonstrating behaviours related to anxiety or high levels of arousal (e.g. displacement behaviours, threat displays). These findings leave us to conclude that emotional or behavioural contagion was not identified in capuchin monkeys under this experimental paradigm; however, systematic variation in attention to specific emotionally valenced stimuli suggests meaningful social information was perceived by subjects.

It is difficult to pinpoint the exact reason for why emotional or behavioural contagion was not identified. First, assuming a true null-result, capuchin monkeys might not use the behaviour of conspecifics to directly cue their own

behavioural or emotional response, without that behaviour being directed toward the observer in a communicative way (i.e. threat display in the direction of an observer). The video stimuli presented in this experiment were recorded to give the impression of a monkey being eavesdropped upon. This was intentional, as they were designed to elicit automatic behavioural or emotional contagion in response to the same behavioural or emotional state, rather than to elicit a complementary response to a communicative gesture. It is therefore possible that this finding reflects a true negative result indicative of ecologically valid capuchin behaviour. Evidence of behavioural contagion found in the study of neighbour effects (Videan et al., 2005; Watson & Caldwell, 2010) is often triggered through vocalisations with communicative functions. On the other hand, many of the behaviours displayed by monkeys in the stimuli may hold no communicative value to a third party observer (e.g. grooming, scratching, foraging, etc.). Threat displays were observed in the videos which signal aggression towards the recipient of such a display, however, it is unclear whether the signal holds the same value to a third-party observer. It is also possible that the individual monkeys presented in the videos could have influenced responses. Dominant males from each group were always present in the videos, sometimes alone, sometimes with other monkeys, and it is possible that the relationships between the subjects and the individuals in the video could mediate a behavioural or emotional response. For example, emotional co-ordination between mother-infant pairs has been found in humans and birds

(Edgar, Lowe, Paul, & Nicol, 2011; Waters, West, & Mendes, 2014), and it is unclear whether this emotional contagion might extend to unrelated group mates. Some of the younger subjects in this study were observing first-degree relatives in the videos (e.g. mother, father, son, brother), however, an unreported examination of these monkeys' reactions to those specific stimuli identified no systematic variation in any direction.

It could be argued that subjects could not perceive the social content of the videos. The technology used to record and present video stimuli is produced for human viewing and it is difficult to know whether nonhuman animals perceive the same information as human experimenters (D'Eath, 1998). However, capuchins have been found to react to social stimuli presented in video monitors. For example, Anderson and colleagues (Anderson, Kuroshima, Paukner, & Fujita, 2009) found that monkeys observing themselves in video recordings noticeably altered their behaviour and in some cases performed communicative facial gestures toward the recordings. Our subjects were never observed responding in this way. In the study by Anderson et al. (2009), subjects were more likely to direct facial displays towards videos showing monkeys directly facing the camera, but the monkeys in our stimuli were not orientated in this way. A substantial body of evidence suggests that video playback is successful in eliciting context specific social effects from monkeys and apes (Anderson, Myowa-Yamakoshi, & Matsuzawa, 2004; Parr, 2001;

Paukner & Anderson, 2006), but it is nonetheless possible that the stimuli were not ecologically valid. A recent study with the same population of capuchin monkeys tested here found that behavioural responses to a picture of a conspecific did not match the reaction to the real conspecific (Morton et al., under review). The authors attribute this finding to absence of other relevant cues (e.g. movement, sounds, smell, etc.), and the same factors may have confounded the results found here. It is possible therefore that the presentation to subjects of moving images of conspecifics in an unusual context lacked the auditory and other sensory information necessary for authentic emotional or behavioural reactions.

It is important to also consider that the interval between the onset of the stimulus and the collection of the second saliva sample did not allow an optimal measurement of cortisol variation. This interval was limited due to welfare considerations for the subjects, and while changes in cortisol can be identified within ten minutes of arousal, peak cortisol levels are identified 20 to 40 minutes after the occurrence of a stressor (Dickerson & Kemeny, 2004). It may then be that the interval was not sufficient to identify subtle changes in cortisol caused by stimuli. Overall, it is difficult to distinguish between a genuine null-result and an insensitive method. However, the finding that monkeys attended significantly more to stimuli presenting a group-mate in an anxious behavioural state suggests that some element of these specific stimuli

were of interest to the monkeys. While it is tempting to interpret this observation through an anthropomorphic lens and claim evidence of nonhuman schadenfreude, a more parsimonious interpretation is that the behaviours exhibited by the monkeys in those videos (e.g. high vigilance, threat display, etc.) acted to alert the subject to a potential environmental or social stressor. Increased attention to these videos may have then been an effort to identify this stressor. This evidence of systematic attention to stimuli does suggest that some aspects of specific stimuli hold significant interest to observers.

A secondary goal of this study was to examine qualities of stress hormones in capuchin monkeys. To this end, evidence of increased levels of cortisol in samples collected in the morning and early afternoon complements previous findings of cortisol circadian rhythms in primates (Chan & Debono, 2010; Heintz et al., 2011), and validates the use of salivary cortisol as a measure of meaningful physiological change. It has been argued that improved animal welfare generates more reliable and valid empirical data (Ash, 2014), and in this sample, monkeys' salivary cortisol did not increase significantly over the course of a research session on average, indicating that the procedures used to study these capuchin monkeys was not detrimental to the participant's welfare in general. It could be argued that the second hormone measure represents the rise but not the peak of cortisol concentrations, but half of monkeys' median

values from the second sample were lower than median baseline measures (see Table 2), suggesting that this non-significant result is not indicative of a trend in increasing cortisol. When examining individual variation in cortisol levels only two monkeys were identified as having significantly elevated cortisol levels at the end of the session on average. Interestingly, both monkeys were enthusiastic subjects in research sessions. One of these monkeys, Junon, has been taking part in cubicle research for a number of years (e.g. see Morton, Lee, & Buchanan-Smith, 2013) and did not display obvious signs of anxiety throughout research sessions. Similarly, the other monkey who displayed an increase in cortisol levels, Ximo, was anecdotally the most reluctant to leave the cubicle area once the research session was complete. During research sessions these specific monkeys demonstrated no obvious signs of anxiety; however, examining behavioural correlates of cortisol identified some interesting effects. Lower vigilance behaviour during a research session predicted a reduction in cortisol over the session. While difficult to conclusively explain the reason for this finding, one interpretation is offered here. During some research sessions a monkey might be more motivated to attend to activities in their social group. If this is the case, separation from their group may lead to an increase in stress hormone levels and also increased interest in activity outside of the research cubicles (which is what the measure of vigilance examined). Also, comfort in the cubicle (measured as the number of times a subject signalled their intention to leave the research cubicles) was a marginally significant predictor of an

increase in cortisol. This suggests that the measure of comfort used in this study was a valid one, and future researchers may want to more stringently adhere to these signals performed by monkeys. However, while a small number of monkeys showed a significant increase in stress hormone levels, the majority demonstrated no such change, and indeed half of the monkeys showed a (non-significant) decrease in median cortisol level through the research session.

While behaviours performed by monkeys during the research sessions might be related to real-time change in cortisol, behaviour may also be indicative of a monkey's general arousal at the time of the research session. A reduction in some behaviours were found to predict higher levels of average cortisol. For example, when cortisol was higher both vigilance and attention to the video stimuli was reduced. Also, when cortisol levels were higher, a marginally significant reduction in scratching behaviours was identified. The identified relationships can be interpreted in two ways. Higher levels of arousal might reduce some activities (i.e. attention to stimuli, vigilance). This reduction in certain behaviours may be indicative of a freeze response that occurs when animals are threatened (e.g. rats, Blanchard, Flannelly, & Blanchard, 1986; humans, Roelofs, Hagenaars, & Stins, 2010). On the other hand, animals with lower cortisol levels may be using certain behaviours (e.g. vigilance, scratching, attention to stimuli) to reduce their stress levels. If this is the case, the behavioural predictors of stress are better interpreted as coping mechanisms.

Under this interpretation, monkeys with higher levels of cortisol may not be coping with the stress as well as monkeys displaying increased activity levels. Indeed self-reported stress levels have been found to be reduced in men that are observed to perform increased displacement activities (Mohiyeddini, Bauer, & Semple, 2013; Mohiyeddini & Semple, 2013). Future research should aim to differentiate between these interpretations, but it is important to recognise that regardless of which interpretation is correct, this finding has significant implications for the study of emotion through behaviour. Based on previous research on the behavioural correlates of stress (e.g. Maestripieri, 1993; Maestripieri et al., 1992; Polizzi di Sorrentino, Schino, Tiddi, & Aureli, 2012), one might conclude that when monkeys are more vigilant and scratch more often in relative terms, they are also likely to be "more stressed". Here, the hormone profiles of subjects when itchy and vigilant were lower than when those same monkeys were less vigilant and less itchy. The use of behaviour to infer emotional state is problematic, and the findings of this study suggests caution should be practised when examining emotion through behaviour.

This study of emotional contagion in capuchin monkeys raises more questions. It may be that evidence of emotional contagion identified through neighbour effects (e.g. Watson & Caldwell, 2010) reflects meaningful behavioural synchronisation without a mediating emotional component. It may be that the emotional content in a monkey's behaviour acts only as a first-step towards

cuing an adaptive, congruent behavioural response in an observer. This first-step may have been observed in this study. These questions have yet to receive conclusive answers, but the study of emotion in animals is a challenging task. It is clear that we are far from completely understanding emotional and behavioural transfer, and the interaction between the two. In the next chapter, this link between emotion and behaviour is examined further by addressing a simple behaviour that has taken on considerable importance in the study of primate emotion: Scratching.

Chapter 6: Contagious scratching in capuchin monkeys

The relevance of itch to physical and psychological well-being has long been recognised, and as early as 1660 was defined as "an unpleasant cutaneous sensation which provokes the desire to scratch" (Hafenreffer, 1660, cited in Rothman, 1941). Today, this centuries-old definition regularly appears in the scientific literature and captures an important dualism. An itch is defined both by the sensation in the skin and the behavioural action that quells discomfort. When considering itch in primates it is important to recognise both the sensory and motor aspects of itch for one important reason. While it is assumed that animals get itchy, scratching behaviour in nonhuman animals is often discussed without invoking the probable cutaneous origin. The exploration of itch is then restricted to those species that can describe the sensation (i.e. humans), and while it is true that a sensation of itch does not necessarily lead to a scratch (e.g. scratching responses can be inhibited, Rosenbaum & Ayllon, 1981), it is less clear if scratching occurs without the sensory trigger. In humans for example, scratching rates are correlated with reported itchiness (Holle et al., 2012), and a causal understanding of how scratching alleviates itch is beginning to be understood (Yosipovitch, Fast, & Bernhard, 2005). Without evidence to the contrary then, it is reasonable to assume that an observed scratch, in the majority of cases, is elicited by an uncomfortable sensation of itch.

Scratching must therefore be examined in the context of itch, especially as scratching and other self-directed grooming behaviours as used as indices of emotional arousal in nonhuman primates (Maestripieri et al., 1992; Polizzi di Sorrentino et al., 2012). While a correlational relationship between observable behaviour and underlying emotion is undeniably useful, a complete understanding will only emerge from careful consideration of the entire process of itch, incorporating a broad literature on physiological, neurological and psychological factors. With this goal in mind, I will examine both the sensation of itch and its observable motor response with a special focus on scratching as a displacement behaviour.

A chronic or acute sensation of itchiness, formally called pruritus, can be rooted in a skin disorder, a disease of another organ, damaged nerve fibres, or psychological causes (for a review see Ikoma, Steinhoff, Ständer, Yosipovitch, & Schmelz, 2006). Once believed to be a mild form of pain, it has now been established that while some mechanisms are shared, the sensation of pain and itch have unique neurophysiological pathways (Mishra & Hoon, 2013), and indeed some elements of these itch pathways are beginning to be mapped (Andrew & Craig, 2001; Davidson & Giesler, 2010; Davidson et al., 2012; Namer et al., 2008). The sensation of itch can be rooted in a number of non-cutaneous factors (e.g. chronic kidney failure, Mettang, 2010), but most itches originate in

the skin. An irritant, whether physical or chemical, triggers a series of physiological steps that leads to itch being registering in the brain where an appropriate motor response is planned (Patel & Dong, 2010). One commonly explored pathway is mediated by histamine. An irritant or allergen triggers the release of histamine from mast cells in the skin facilitating a local immune response and simultaneously stimulating peripheral C-fibres (i.e. unmyelinated sensory nerve fibres) that relay the sensation of itch to spinal nerve cells (Andrew & Craig, 2001; Davidson & Giesler, 2010; Jutel, Watanabe, Akdis, Blaser, & Akdis, 2002; Schneider, Rolli-Derkinderen, Arock, & Dy, 2002). While histamine-induced itch is the most commonly studied pathway, itch can also be evoked through mechanical (Fukuoka, Miyachi, & Ikoma, 2013) and electrical means also (Ikoma, Handwerker, Miyachi, & Schmelz, 2005), and some components of these pathways differ from the histamine mediated route (Davidson & Giesler, 2010; Davidson et al., 2012; Namer et al., 2008). For example, it has been found that different afferent C-fibres relay histamine and non-histamine-induced itch (e.g. Davidson et al., 2007; Namer et al., 2008). Histamine induced itch does not activate any itch-specific brain region, but a number of regions associated with itch have been dubbed the itch-matrix (Mochizuki et al., 2007). The only study to examine the neurophysiology of psychologically induced itch examined the activation of brain regions when watching someone scratch and discovered that the same region activated during the sensation of itch were stimulated when watching someone else

scratch (Holle et al., 2012). Thus, the simple definition of itch cited in the introduction betrays a complex phenomenon that occurs under a surprising range of conditions, and while itch is not yet entirely understood, we have learned a lot about the proximate mechanisms over the preceding decades.

But why itch in the first place? In certain circumstances an itch can be adaptive. A localised sensation on the skin alerting an animal to the presence of an irritant (e.g. an ectoparasite or chemical) may lead to its removal through scratching or self-grooming. Indeed, the frequency of scratching, as part of a broader grooming repertoire, increases in animals exposed to ectoparasites (Eckstein & Hart, 2000; Loewenstein, Ludin, & Schuh, 2006), and animals that are prevented from self-grooming and scratching have higher parasite loads (Mooring, McKenzie, & Hart, 1996; Murray, 1987). In cases of pathogen induced itch, or itch caused by a disease of the skin or another organ, the role of scratching is less clear, as in these cases skin may be damaged or scarred (e.g. Oaklander, Cohen, & Raju, 2002). In fact, it is this potentially harmful form of itch that has largely driven research into the proximate mechanisms of the phenomenon while adaptive itch is ignored.

Our understanding of multiple itch mechanisms is advancing, but there is little

evidence that these inroads have influenced the study of itch in other empirical spheres. The study of nonhuman primate behaviour is a field where the complementary motor response of itch has taken on complex and significant meaning, allowing human observers insight into the unobservable emotional states of their subjects.

A scratch may displace a parasite or a piece of detritus embedded in fur, but it is a displacement behaviour in another sense. Displacement activities are behaviours that appear "out of context with the behaviour which closely precedes or follows them, either in the sense that they do not seem functionally integrated with the preceding or following behaviour or that they occur in situations in which causal factors usually responsible for them appear to be absent or at least weak" (Delius, 1967, p 1294). We do not entirely know why displacement behaviours occur (Anselme, 2008), but they are performed by a range of taxa (Diezinger & Anderson, 1986; Huxley, 1914; Tinbergen & Iersel, 1947), and are correlated with instances of motivational conflict, behavioural thwarting, and stress (Delius, 1967; Maestripieri et al., 1992). Displacement activities take on many forms and can relate to feeding (Raber, 1948), parental care (Sevenster, 1961), or body care (Maestripieri et al., 1992). In primates, displacement behaviours often take on the latter's form; self-directed scratching, grooming, yawning, and body rubbing are all classed as

displacement behaviours (Maestripieri et al., 1992). The study of displacement

behaviours was popular in the middle of the last century (e.g. Cohen & Price,

1979; Sevenster, 1961; Tinbergen & Iersel, 1947; for a review see Zeigler, 1964),

but while no satisfactory proximate or ultimate explanation of displacement

behaviours emerged, interest has dwindled since the early 1970s (for an

example of the decline in use of the terms related to behavioural displacement

activities see Figure 6.1). However, recent studies of emotion and welfare in

nonhuman primates have benefitted greatly from examining this class of

behaviour.

In the late 80s and early 90s, a number of studies reported the observation that

self-directed displacement behaviours were often performed by primates when

stressed (Aureli & van Schaik, 1991; Pavani, Maestripieri, Schino, Turilazzi, &

Scucchi, 1991; Schino, Maestripieri, Scucchi, & Turillazzi, 1990; Troisi & Schino,

1987). Based on this evidence, Maestripieri et al. (1992) suggested displacement

behaviours could be used as reliable indicators of anxiety in primates. Both

pharmacological and behavioural observations lend support to this assertion.

Anxiogenic drugs administered to long-tailed macaques (*Macaca fascicularis)*

increased displacement behaviours while anxiolytic treatments reduced their

frequency (Schino, Perretta, Taglioni, & Troisi, 1996). Similarly, anxiolytic

treatments administered to marmosets (*Callithrix jacchus and C. penicillata*)

reduced subsequent scratching bouts when the monkeys were placed in stressful scenarios (e.g. presented with novel stuffed animals or a novel conspecific, Barros, Boere, Huston, & Tomaz, 2000; Cilia & Piper, 1997).

Figure 6.1. Frequency of terms related to displacement behaviours in the Google n-gram database which contains a digital record of over 15 million books (~12% of all books ever published; Michel et al., 2011) made freely available to search for the frequency of words or strings of words (see Michel et al., 2011). Result below show the combined frequency of the following terms: displacement activity, displacement activities, displacement behaviour, displacement behavior.
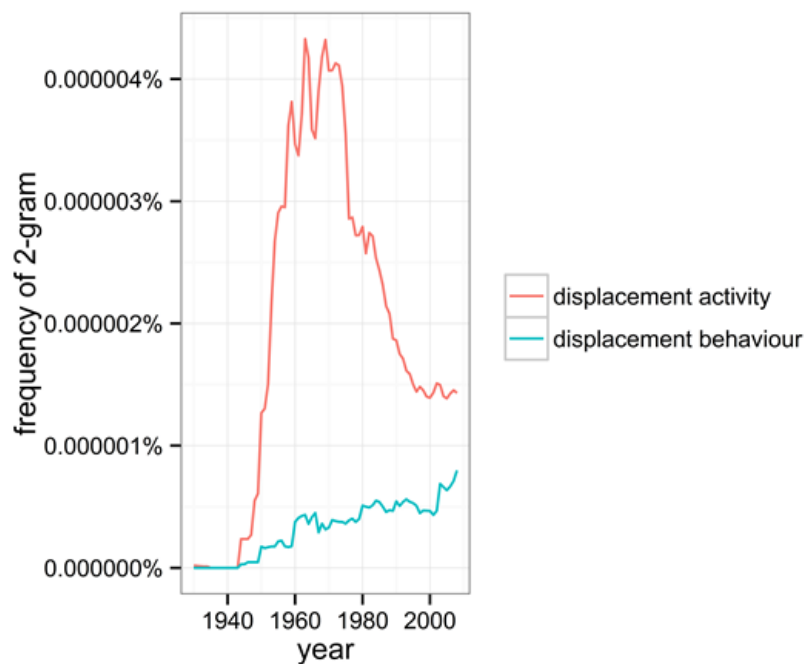
There is also behavioural evidence linking the frequency of displacement behaviours to anxiety. When infant rhesus macaques (*Macaca mulatta)* are in dangerous situations their mothers scratch more often (Troisi et al., 1991), and when *M. fascicularis* are paired with unfamiliar conspecifics scratching rates are also seen to increase (Schino et al., 1990). Similar evidence of a relationship between anxiety and displacement behaviours has been reported for capuchin monkeys (*Cebus apella nigritus*, Polizzi di Sorrentino et al., 2012, lemurs (*Lemur cata*, Sclafani, Norscia, Antonacci, & Palagi, 2012), chimpanzees (*Pan troglodytes*, Leavens, Aureli, & Hopkins, 2001; 2004), and baboons (*Papio anubis*, Castles, Whiten, & Aureli, 1999), and based on these findings, researchers have used scratching and other displacement behaviours when examining stress in captive animals. The frequency of total displacement activities performed are often used as one proxy measure of anxiety (e.g. Fagot, Gullstrand, Kemp, Defilles, & Mekaouche, 2013; Plowman, Jordan, Anderson, Condon, & Fraser, 2005; Pomerantz & Terkel, 2009), but scratching is sometimes measured and/or analysed independent of other behaviours (e.g. Carder & Semple, 2008; Rimpley & Buchanan-Smith, 2013). While certain displacement behaviours defined in original theoretical papers on the displacement-emotion relationship may not be included in ethograms (e.g. yawning, body shaking, self-grooming), scratching is almost always incorporated, possibly due to the relative frequency and conspicuousness of these behaviours.

There is also some evidence that self-directed displacement behaviours are good predictors of anxiety in humans. Waxer (1977) found that psychiatric patients who scored higher on measures of anxiety performed a significantly higher number of non-communicative hand-gestures including self-stroking. When comparing nonverbal behaviours of psychiatric patients and control participants, Fairbanks and colleagues (1982) found that psychiatric patients displayed higher frequencies of grooming behaviours (e.g. hair or face touching). Similarly, experiences more likely to induce anxiety increase self-directed behaviours. For example, when the topic of conversation in a psychiatric interview is of particular emotional relevance to the interviewee, hand-to-body self-touching rates increase (Shreve et al., 1998, cited in Troisi, 2002).

A wealth of evidence supports the claim that self-directed behaviours are reliably related to anxiety in primates. While the validity of this finding is not in question, further steps are necessary to properly understand this link and provide satisfactory ultimate and proximate explanations of how the underlying emotion states of an animal can predictably lead to a certain behavioural response (see discussion section in Chapter Five). As scratching is central to much of the literature on this topic it is surprising that further attention is not paid to the literature concerning itch in humans, or indeed the

broader literature on physiological or autonomic changes correlated with stress responses.

Displacement rates are certainly influenced by social factors. Scratching rates increase following aggressive encounters (Aureli & van Schaik, 1991; Daniel, Santos, & Vicente, 2008), when an individual is closer to a more aggressive conspecific (Polizzi di Sorrentino et al., 2012), and during or after other socially stressful events (Cilia & Piper, 1997; Sclafani et al., 2012). However, another social phenomenon may influence the performance of displacement behaviours like scratching. Social facilitation and behavioural contagion are processes where a behaviour performed by one individual increases the likelihood that the same behaviour (or class of behaviours) is performed by an observer (Hoppitt & Laland, 2008a). In human and nonhuman primates, the contagious nature of yawning has received the most interest (e.g. Anderson, Myowa-Yamakoshi, & Matsuzawa, 2004; Campbell & de Waal, 2011; Millen & Anderson, 2011; Paukner & Anderson, 2006). However, other displacement behaviours are also socially facilitated. A number of studies have found that preening (a well-established displacement behaviour in birds) is socially facilitated (Hoppitt et al., 2007; Palestis & Burger, 1998), and there is growing evidence that scratching is contagious in human and nonhuman primates.

Evidence of a contagious scratching effect in humans is convincing. Healthy adult observers experience the sensation of an itch and scratch more often after seeing someone else scratch (Holle et al., 2012). Indeed, the use of fMRI scanning when observing someone else scratch has found that brain regions active when scratching are also active when observing someone else scratch (Holle et al., 2012). Contagious scratching has also been examined in nonhuman primates. An early study of action imitation found that a long-tailed macaque could easily learn to scratch when an experimenter scratched (Mitchell & Anderson, 1993). In the first study of contagious scratching, Nakayama (2004) found that Japanese macaques (*Macaca fuscata*) would increase scratching rates after observing an alert groupmate scratch. A more recent study examined contagious scratching in rhesus macaques (Feneran et al., 2013). When housed in pairs, it was found that macaques were more likely to scratch in the two minutes following a cagemate's scratch. Under experimental conditions monkeys were also more likely to scratch after watching video footage of another monkey scratching. However, it is unclear how wide-spread this contagious scratching effect is, as a recent investigation of contagious behaviours in nonhuman great apes found no evidence of contagious scratching after viewing a conspecific or human experimenter scratch (Amici et al., 2013). The occurrence of contagious displacement activities (e.g. yawning, preening, and scratching) is problematic for the study of displacement behaviours as measures of emotion.

Given that scratching is both a reliable predictor of emotional arousal in at least some species of primates, and socially transmissible between groupmates, the question arises whether corresponding emotional states may also be transmitted during contagious scratching events. The emotional contagion interpretation of scratch contagion is an interesting one, especially as emotional contagion has been identified in a number of species. As already mentioned in Chapter 5, Buchanan et al. (2012) found that cortisol levels measured in humans observing someone experience a stressful event (e.g. an oral presentation) increased in proportion to the levels of cortisol measured in the stressed speaker. Similarly, second order emotional contagion has been identified. Participants watching the face of another individual, who is watching a video of an actor producing joyful or fearful expressions, respond with facial expressions and skin conductance levels that correspond to the emotions portrayed by the actor (Dezecache et al., 2013). This ability to pick up on the emotions of others is present from an early age. Babies mirror the physiological stress response of a mother that has undergone a stressful experience (Waters et al., 2014), and a similar but contralateral effect was found in mother hens who became distressed after observing their chicks display stressful behaviours (Edgar et al., 2011). It seems emotions are also transmitted between nonhuman primates as agonistic and affiliative vocalisations from neighbouring captive primates affect the behaviours of the individuals listening to these calls (i.e. agonistic calls increase aggressive behaviours, affiliative calls increase

grooming behaviours, etc.; Baker & Aureli, 1996; Watson & Caldwell, 2010; Watson, Buchanan-Smith, & Caldwell, 2014). If auditory cues influence behaviour in a manner indicative of emotional contagion it is conceivable that a visual cue (i.e. a displacement behaviour like scratching) could induce a similar effect.

In the current study the investigation of contagious scratching is extended by studying this effect in a species of New World primate for the first time. Video recordings of conspecifics were presented to subjects. Some video stimuli displayed monkeys scratching themselves, while others did not. The primary hypothesis was to examine if rates of scratching were higher after observing scratching groupmates. Scratching contagion might be a behavioural artefact of emotional contagion and so is a behavioural example of emotional contagion. If this is the case a broader range of stress-related behaviours might be influenced by the scratching stimuli.

Methods

Animals and research site

Ten tufted capuchin monkeys (*Sapajus sp.*) were tested (eight males, mean age = 6.33 years; SD = 3.43). All monkeys were housed in one of two mixed-species

groups (with squirrel monkeys, *Saimiri sciureus*) at the Living Links to Human Evolution Research Centre at Edinburgh Zoo, Scotland (for a comprehensive description of the facility see Chapters Two and Four, also MacDonald & Whiten, 2011). The monkeys were never food or water deprived, and all rewards offered during research sessions were supplementary to their diet. Ethical approval was granted by the University of Stirling Psychology Ethics Committee.

Materials

Eight research cubicles arranged in a connected 2X4 matrix act as a corridor between the monkeys' indoor and outdoor enclosures (each cubicle measures 49.5 cm X 52.1 cm X 51.4 cm). Partitioning slides inserted between cubicles allow monkeys to be separated from their groupmates for research purposes, and for this study subjects were granted access to two adjacent cubicles. To create stimuli videos clips of monkeys were recorded on a Sony Mini Digital Video Camera. The video stimuli were presented using Microsoft PowerPoint, and presented to monkeys on a 19"monitor.

Stimuli

As dominant monkeys did not take part in research sessions, these individuals were recorded for use in the video stimuli. As the subjects were sampled from two different captive groups, stimuli videos were created for each group with subjects only ever presented with footage of monkeys from their own group. When a scratching event (defined as the "movement of the fingertips repeatedly across the same skin area"; adapted from Feneran et al., 2013, p 27) was identified, the relevant section of video was edited to a 10-second clip. In total, five 10-second clips were created for each group. All clips included the alpha male from the relevant group. For one group, two clips contained footage of the alpha male with both the alpha and beta females (each carrying an infant). For the other group, two clips contained the alpha male and alpha female. Each 10-second clip was subsequently edited into two 5-second clips; one clip containing a scratching event, the other containing the same monkey/s but with no scratching event. In six of the ten clips the scratching event took place in the first five seconds, with the control clip being the subsequent five seconds, and in the remaining four the scratching event took place in the final five seconds and therefore the control clip was the earlier segment. No change in behaviour was apparent between control clips taken from before or after the scratching event. Five scratching clips were combined to create the 30s stimulus clips and five neutral clips were used for each of the control stimulus clips. Each 5s video clip was followed by an olive-green screen for one second.

Procedure

Each monkey completed two sessions. Once the subject was separated, and before the session commenced, the video monitor was placed approximately 50 cm from one of the two cubicles in use. A black screen accompanied by a beep signalled the beginning of the session (see Figure 6.2; a beep also signalled the start and finish of a stimulus presentation and delivery of a food reward). After 15 s, a single reward was offered to the monkey by hand. At 30s, the first video clip was presented. A black screen was presented from 60s to 90s, and a single reward was offered at 75s. The second clip was presented at 90s, followed by a black screen at 120s. A single, final reward was offered at 135s. For their first session half of the subjects received the scratching clip first, and each monkey received both possible orders of presentation over the two sessions. Due to experimenter error one monkey (Ximo) received the same order of presentation during both sessions. Ximo was tested a third time with the alternate presentation order. Including data from this monkey's 1st and 2nd sessions (not counterbalanced), or 1st and 3rd sessions (counterbalanced) altered the results of statistical tests, so data from all three sessions were analysed. However, for the sake of transparency in statistical reporting, all results are reported.

Figure 6.2: Experimental procedure for each session; food reward (half a peanut) presented at 15, 75, and 135s. Order of stimuli was counterbalanced across subjects, and each subject experienced both orders over two sessions.
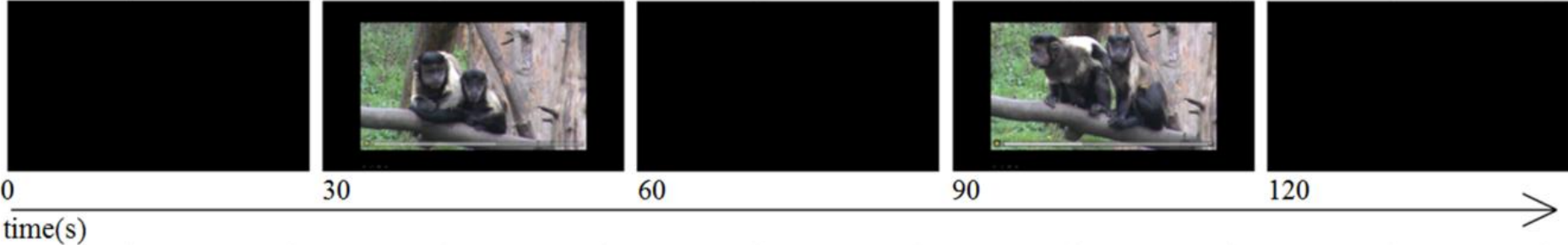
Each monkey was continually recorded on video throughout each session. Videos were subsequently coded by two observers for relevant behaviours (see Table 2 for definitions). Due to the results of Chapter Five, where an increase in cortisol was related to a reduction in vigilance behaviour and a marginally significant increase in comfort related door touching (see description in Table 1), these behaviours were particularly relevant to an observation of emotional change. Behaviours exhibited during the 60-sec period following the start of the scratching clip were combined across the two sessions for each monkey. Behaviours coded following the control clip were similarly managed. Cohen's Kappa was calculated for 50% of the data and interobserver reliability was high ($Kappa_{scratch} = 1$; $Kappa_{comfort} = .70$; $Kappa_{vigilance} = .86$, $Kappa_{activity} = 1$). Each coder's dataset was analysed independently and no differences were found in terms of statistical significance or direction of the reported effects. Results are reported for only one set of data. To account for a small sample size bootstrap procedures were incorporated (10,000 iterations) when comparing between conditions (scratching vs. control) and confidence intervals for paired t-tests are reported (two-tailed unless otherwise specified).

Table 6.1: Behaviours coded to examine contagious scratching and emotional contagion.

Behaviour	Definition
Scratch	The "movement of the fingertips repeatedly across the same skin area" (adapted from [13 p. 27]); more than 3s without scratching had to elapse before a scratching bout was coded as a new event (a similar rule was applied to measures of vigilance and comfort).
Activity	The number of times the monkey passed from the first cubicle to the second.
Vigilance	Vigilance was measured as the number of times the subject looked through the holes in the opaque partitioning slides.
Comfort	If the monkeys persistently pushed on the partitioning slide (i.e. pushed on the slide more than once without changing their behaviour) the researcher would open it to allow the monkey to leave the cubicle. While no monkey did this, the number of times each monkey performed this behaviour was recorded as a measure of how comfortable the monkey felt during the session.

Results

Three monkeys did not scratch during any session (see Figure 6.3). When data from all of Ximo's sessions are analysed, monkeys were found to have scratched significantly more often in the scratch condition (mean = 1) than the control condition (mean = .5), (n=10, p = .020, mean difference = 0.5, 95% CI = 0.2 - 0.8). This overall result is the same if the analysis is re-run with only Ximo's 1st and 3rd sessions, however, the difference in average scratching rate between conditions drops below significance if Ximo's 1st and 2nd session are analysed (n = 10, p = .126; mean difference= 0.4, 95% CI = 0 - 0.8). The direction and significance of all further statistical comparisons do not differ based on Ximo's data so results are only reported for an analysis that includes all sessions.

Analyses of other stress-related behaviours revealed no significant differences between conditions for measures of vigilance (mean$_{scratch}$ = 1.8, mean$_{control}$= 1.8; p= 1, see Figure 6.4a), activity (mean$_{scratch}$ = 1.6, mean$_{control}$= 2.0; p = .533, Figure 6.4b), or comfort (mean$_{scratch}$ = 1.5, mean$_{control}$= .9; p = .265, Figure 6.4c).

Figure 6.3: Total number of scratches by each monkey in each condition (Ximo scratched once following the control video in his second session, and scratched once following the scratching video in his third session).
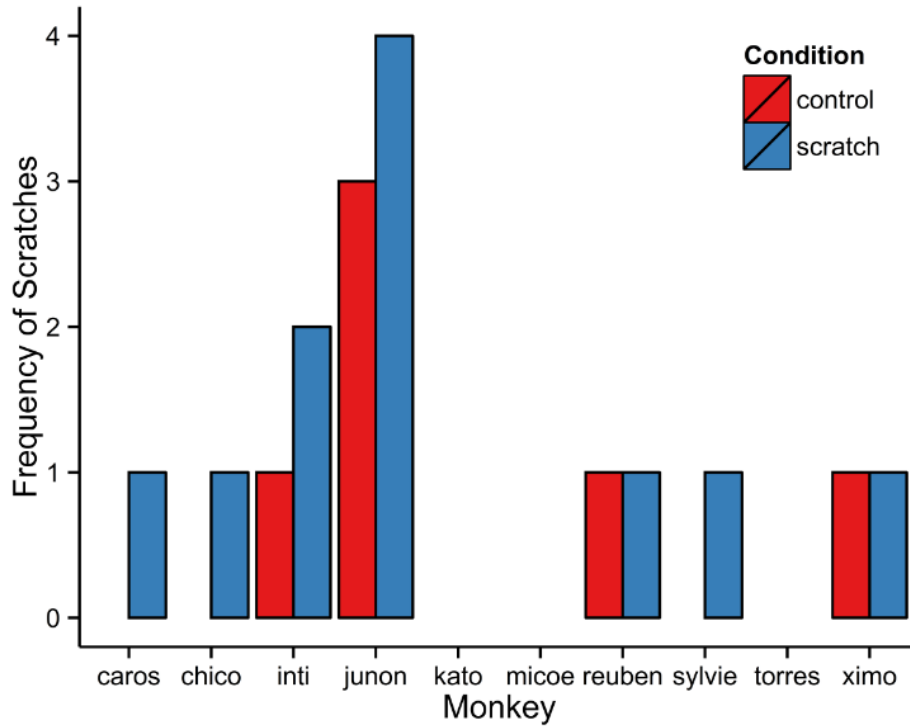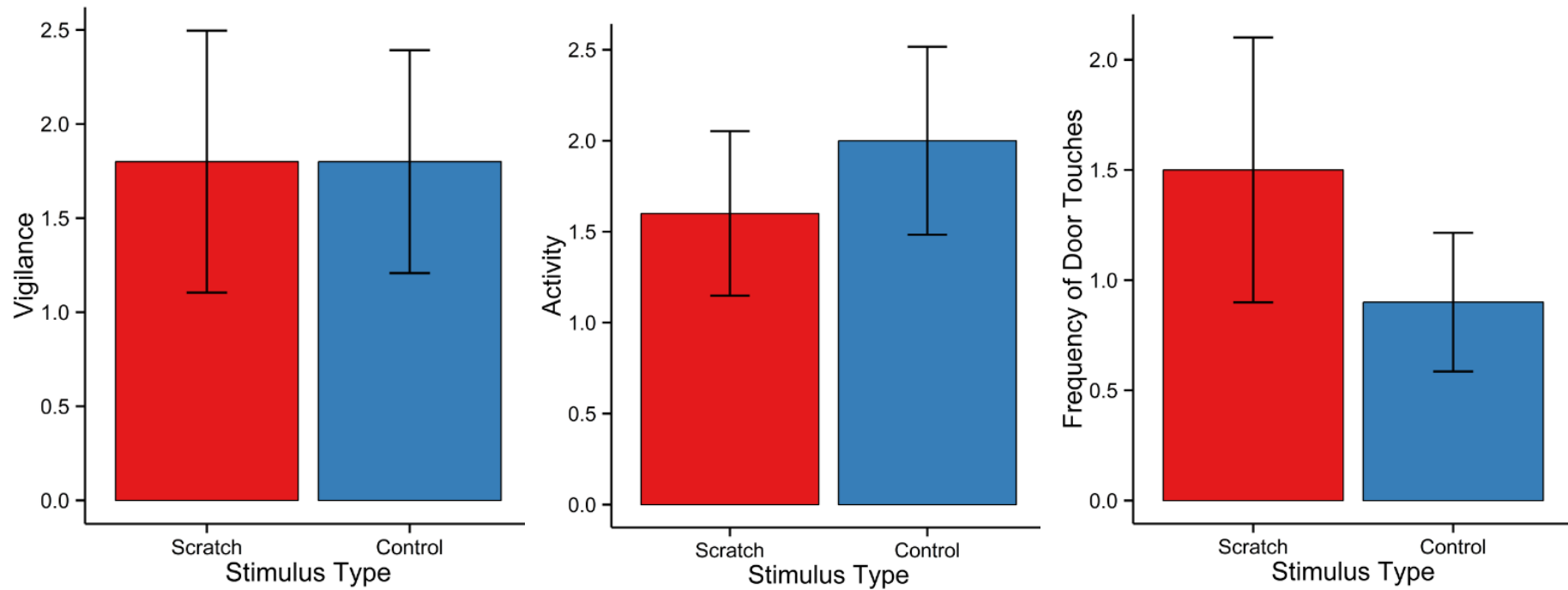
Figure 6.4: Mean frequency of: a) vigilance behaviour, b) activity levels, and c) comfort, for each type of stimulus. Error bars represent standard errors of mean values. For definitions of behaviours see Table 6.1.

Discussion

When presented with a video of groupmates scratching, capuchin monkeys were more likely to scratch than when they were presented with a video containing no scratching, a finding consistent with previous reports of scratching as a contagious behaviour in monkeys and humans (Feneran et al., 2013; Holle et al., 2012; Nakayama, 2004). However, given the marginal nature of this result, caution is urged. Under the most conservative analyses, five out of six monkeys that showed differential rates of scratching towards stimuli scratched more often to scratching stimuli. While on the surface this result is suggestive of scratching contagion, the low statistical power associated with small sample size increases the likelihood of a type II error, and increases the influence of single data points in determining p-values. Thus, the evidence of scratching contagion reported here is relatively preliminary and further research is necessary to reliably conclude an effect of scratching contagion in New World primates. Given evidence that scratching is transmitted in a contagious manner in humans and Old World monkeys, it may be unsurprising that capuchin monkeys also demonstrate a propensity to contagiously scratch. However, previous research on nonhuman great apes failed to find a scratching contagion effect (Amici et al., 2013). Further study is necessary to develop a complete understanding of the phylogenetic distribution of contagious scratching. If this effect is absent from great apes we must ask why this is the case, given evidence from other related species.

While preliminary evidence of contagious scratching was found in this sample, no other stress-related behaviours were found to vary across conditions, suggesting that contagious scratching occurs independently of emotional contagion. While social contagion through vocalisations suggests that captive primates are influenced directly by emotionally salient stimuli (Baker & Aureli, 1996; Watson & Caldwell, 2010), here we see that one form of behavioural contagion, triggered by a visual cue, may occur without accompanying emotional contagion.

If the primary function of scratching is to remove ectoparasites, then contagious scratching may act to increase sensitivity to external cutaneous stimulation; i.e. increasing the chance of detecting an ectoparasite. On two occasions during or immediately after observing the scratching video monkeys scratched themselves to remove detritus from their skin. Therefore, the observation of a groupmate scratching may act to increase sensitivity to cutaneous sensations, and while this increased sensitivity may often lead to unwarranted scratching, benefits gained by improving parasite detection and removal may be adaptive in the long run. Scratching has become surprisingly significant in the study of primate emotion, but mere recognition of a relationship between scratching and anxiety is unsatisfactory (the same applies to other self-directed displacement behaviours). This observation has allowed researchers examine otherwise

unobservable psychological phenomena in nonhuman primates. However, if we do not fully understand the mechanism underlying this relationship we risk confounding influences from factors we do not appreciate. Interest in displacement activities may have waned in recent decades, but with the use of such behaviours continuing to thrive in the field of primatology, the proximate and ultimate cause of displacement behaviours may be best explored in the context of the study of primate emotion. While it is still unclear whether contagious scratching is a general phenomenon found throughout the primate order, the behavioural contagion of displacement behaviours in some nonhuman primates naturally leads us to enquire whether emotional contagion may also be taking place. In nonhuman primates scratching contagion could be mediated in at least two ways: 1) the underlying emotional state of one individual could be passed to another leading to observable behavioural contagion, or 2) a socially transmitted sensation of itch serves to synchronise and enhance parasite detection. The central question is therefore whether emotional state is transmitted during cases of contagious scratching, and in this study no evidence of emotional transfer was identified.

Scratching contagion without emotional contagion creates both theoretical and practical complications when scratching is used to assess the emotional state or welfare of a nonhuman primate, and future research is necessary to tease apart

the function of these behaviourally contagious cases. For example, in the instance of contagious scratching it could be predicted that the contagious scratch elicited by watching a conspecific scratch could serve to promote ectoparasite removal, through increased sensitivity to an itch sensation (in a similar way that negative affect can influence pain sensitisation, (Janssen, 2002). Indeed, in humans, seeing a groupmate scratch is not the only visual stimulus that triggers a scratch. Watching static images of ants, fleas, and skin conditions (Lloyd, Hall, Hall, & McGlone, 2013), or listening to a lecture on the topic of itch also triggers scratching behaviour (Niemeier, Kupfer, & Gieler, 2000). While the little research on contagious scratching has not made it clear whether contagious scratching leads to an overall increase in scratching frequency, or merely creates a tendency for this behaviour to occur synchronously within a group, either possibility could have ramifications for the use of scratching as a behavioural indicator of stress. While we emphasise the importance of examining how contagious scratching may impact the study of emotion in primates, the same caution is urged when examining yawning as a displacement behaviour (e.g. Castles et al., 1999), or indeed any displacement behaviours that also show contagious qualities (e.g. preening in bird species).

The interpretation of behaviour often focuses on cognitive or emotional explanations grounded in the brain. While this approach has contributed much

to our understanding of behaviour, it seems that the contribution of the rest of the body is often side-lined (Barrett, 2011a). The displacement behaviours of most interest to primate researchers are related to body maintenance (e.g. grooming, scratching, body shaking), yet little consideration is granted to internal physiological changes that may underlie such behaviours. While the function of displacement activities are not entirely understood, one possibility first proposed independently by Morris (1956) and Andrews (1956) is that autonomic stress responses affect physiological changes that subsequently trigger observable behavioural routines. It is known that displacement behaviours exhibited by animals are dependent on external stimuli available to the animal at the time of stress or frustration; for example, displacement feeding behaviours are dependent on the availability of food or water in domestic fowl (Raber, 1948). While feeding behaviours are cued by the external stimuli of food availability, some behaviours "seem to be connected primarily from cues arising within the animal's own body" (Bindra, 1959, p 267). Known autonomic responses include increased blood pressure, vasoconstriction of blood vessels in the skin, and sweat production (Kreibig, 2010). With a range of physiological changes taking place when frustrated or anxious it is surprising that little attention has been paid to this mediating variable in the emotion-displacement relationship. While the seminal theoretical paper on the relationship between displacement behaviours and emotion touches upon the possible link between autonomic processes and self-directed behaviours

(Maestripieri et al., 1992, p 974), to our knowledge no research has since directly tested this link. The first theoreticians to propose autonomic processes as a mediating link used the example of preening behaviours in birds (Andrew, 1956; Morris, 1956), but other displacement behaviours could also be triggered by physiological changes (e.g. yawning is thought to function to cool the brain: Gallup, 2011; Massen, Dusch, Eldakar, & Gallup, 2014).

While past theorising suggested displacement activities may take place due to motivational factors (Tinbergen & Iersel, 1947), or to the re-direction of thwarted energy (Bindra, 1959), the explanation of displacement activities (at least in some cases) as standardised responses to homeostatic changes is a rich avenue of research, and an interpretation that makes specific, testable predictions. In the medical literature it is established that stress responses can lead to various expression in cutaneous disorders (Arck, Slominski, Theoharides, Peters, & Paus, 2006; Yamamoto et al., 2009), but this link needs to be examined further in the field of behavioural research. Displacement behaviours may well be a window into the emotions of animals but it is important to understand the pathway between an emotion and an observable behaviour. While evidence of a link between anxiety and self-directed behaviours is robust, when this finding is extended to test hypotheses related to primate emotion (e.g. whether a certain intervention improves animal welfare)

a standardised protocol is advised. Current practices allow great flexibility in the choice of which behaviour to measure and indeed include in subsequent analyses. To reduce bias it is suggested that when displacement behaviours are being observed in primates, all recognised behaviours should be measured (see Maestripieri et al., 1992) and one planned analysis of all pooled behaviours should be performed. If due to some limitation a smaller sample of behaviours is recorded, there is ample support for the sole inclusion of scratching as a proxy measure of emotion (although see discussion section, Chapter Five, for interpretative problems if scratching is a coping mechanism). The standardisation of these methods can only increase our confidence in findings related to the study of primate emotion.

Scratching is a simple behaviour that has taken on a complex significance in the study of nonhuman primate behaviour. In the context of a broader range of displacement behaviours scratching is a useful tool, however, it is argued here that further work is necessary to understand the relationship between displacement scratching and emotion. While contagious effects may act to confound the study of the displacement-emotion relationship, a focussed examination of the interaction between emotion, displacement activities, and behavioural contagion will serve to inform future decisions on the use of displacement behaviours as measures of emotion. Displacement behaviours are

most useful when exploring a primate's emotional reaction to social interactions, but if social interactions themselves increase displacement behaviours through social facilitation or contagion, we need to be cautious in our interpretations. A complete understanding of emotion and displacement behaviours will require consilience between disciplines, consolidating research from neurophysiological and behavioural fields. A concerted research effort has presented the exciting possibility that the underlying emotional states of primates are easily observable. It is hoped that a similarly rigorous approach in the future will enable a richer understanding of those same emotions.

Chapter 7: General Discussion

"There are lifetimes of work awaiting those who wish to provide a deeper understanding of non-imitative processes in social learning which may well be of greater importance in the lives of non-human animals than is imitation" - (Galef, 2013, p 128)

The work outlined in the preceding chapters explored the mechanisms of social learning that are considered to be "less complex". Galef (2013) has claimed that focussing on imitative processes has limited our understanding of a broader range of mechanisms that are at play when animals are influenced by or learn from conspecifics. While debate over how to categorise the various behavioural forms of social learning has led to an increasing consensus (Hoppitt & Laland, 2013; Zentall, 2012), it is incorrect to assume that this equates to understanding these mechanisms. It is of course important to have a common lexicon through which a science of social learning can be communicated, but an understanding of the mechanism and development of many processes of social learning remains lacking (Byrne, 2002a; Galef, 2013). Aiming to understand rather than describe social learning processes is even more important when current definitions are not mutually exclusive (see Call & Carpenter, 2002; Hoppitt & Laland, 2013), and when it is difficult to differentiate between the cognitive mechanisms underlying behavioural observations (e.g. the difficulty in

distinguishing between types of emulation learning; Hopper, 2010). The work presented in this thesis aimed to address some of these problems. Chapters Two and Three examined automatic imitation, and presented results testing hypotheses related to the development of action matching ability. Chapters Four, Five, and Six examined some of the lesser-studied mechanisms of social influence: Group-size effects, neighbour effects, emotional contagion, and behavioural contagion. Far from providing superficial insights, the findings from these studies encourage an approach to social learning that simultaneously embraces the diversity of social learning processes and respects the influence of simpler mechanisms rather than focussing solely on complex imitative learning.

Automatic imitation in capuchin monkeys

The mirror neuron system is thought to facilitate action imitation by mapping observed actions onto a motor representation of that action (Gazzola & Keysers, 2009) and has been studied extensively at the single-neuron level in monkeys (see Kilner & Lemon, 2013). However, little behavioural evidence exists of imitative ability in monkeys. Automatic imitation, the tendency for the observation of an action to cue the performance of that same action, is thought be a behavioural indicator of mirror neuron activity (Catmur et al., 2007; Heyes, 2011; Longo, Kosobud, & Bertenthal, 2008). Therefore, evidence of such an

effect in monkeys is crucial to support the idea that the mirror neuron system facilitates action imitation. Through the use of a stimulus-response compatibility paradigm, the first evidence of automatic imitation in monkeys was identified. Capuchin monkeys performed significantly better on imitative trials than on counter-imitative trials (see Chapter Two, Figure 2.3). While some studies have shown that monkeys are more likely to use actions they have previously observed (e.g. van de Waal & Whiten, 2012; Voelkl & Huber, 2000), the experiment reported in Chapter Two presents the first evidence of this effect using a stimulus-response paradigm. Here, a contribution is made to a growing body of work that suggests monkeys can match the actions of conspecifics (van de Waal & Whiten, 2012; Voelkl & Huber, 2000), but this ability needs to be confirmed in macaque monkeys, as single-celled sampling methods have confirmed the presence of mirror neurons in this family alone (e.g. *Macaca fuscata*, Fujii, Hihara, & Iriki, 2007; *Macaca nemestrina*, Gallese, Fadiga, Fogassi, & Rizzolatti, 1996). The function of mirror neurons is not yet clear (Cook et al., 2014; Giacomo Rizzolatti & Fogassi, 2014). We are learning more and more about what mirror neurons do (e.g. Gallese et al., 1996; Umiltà et al., 2008; Keysers et al., 2003), however, studies of the properties of single neurons tell us little about what mirror neurons are for. If these neurons are involved in imitation, as some have suggested (Giacomo Rizzolatti & Fogassi, 2001), research needs to first demonstrate that animals that have these neurons are able to imitate. This study of capuchin monkeys had taken a small step

towards demonstrating a potential behavioural function of mirror neurons in primate behaviour.

To further enhance our understanding of the cognitive mechanism that facilitates action imitation, two approaches proposed to explain the correspondence problem were explored. In order to gain a better understanding of the cognition of action matching, predictions of an adaptationist approach (the active intermodal mapping, AIM, hypothesis; (Meltzoff & Moore, 1997) were pitted against those of a developmental perspective (the associative sequence learning, ASL, hypothesis; Heyes & Ray, 2000). To test these conflicting approaches to the ontogeny of imitative ability, the reward contingency used in our first study of automatic imitation was reversed; i.e. monkeys that were previously rewarded for imitating were rewarded for performing alternative actions, while monkeys initially rewarded for performing compatible actions were rewarded for imitating. A nativist approach to imitation might predict that in this second block of learning, given the innate mechanism facilitating action matching, an automatic imitation effect should persist. On the other hand, an empiricist perspective on imitation would predict that automatic imitation may be attenuated following counter-imitation learning. The findings reported in Chapter Two are more in line with a learning approach to imitation, with no difference in performance between conditions in

the second bout of learning (see Chapter Two, Figure 2.3). However, it may be that an innate bias towards action imitation also exists in primates, but that this effect does not persist following incompatible experience. Furthermore, the second experiment reported in Chapter Two, where two monkeys were tested on both compatible and incompatible rules over multiple blocks of learning, found little evidence that imitative actions were easier overall. Although one monkey did perform better on imitative trials across all learning blocks this could be attributed to an order effect. This study supports the idea that associative processes may contribute to action imitation, and potentially the primate mirror neuron system.

There is a growing literature suggesting some mechanisms of social learning develop through associative processes (Catmur et al., 2009; Dawson & Chittka, 2014; Leadbeater & Chittka, 2007). Not only do these findings provide insight into the presence of various forms of social learning in animals, but they inform us of the ontogenetic and mechanistic processes underlying this learning. This richer understanding of these processes is a testament to a research effort driven by bottom-up questioning. Discovering that simple processes facilitate connections between sensory-motor representations does not detract from the role these representations may play in other more complex forms of social learning. However, it does advocate caution when predicting potential

functions of mirror neurons, for if mirror neurons are the result of congruently occurring stimuli and actions, they may not serve any particular evolutionary function (Cook et al., 2014).

Automatic imitation in children

Imitative ability in children is vastly different from that of New World primates. Children are skilled imitators from an early age, even imitating causally irrelevant details of action sequences at the age of three (McGuigan et al., 2007). An ASL view of imitation predicts that synchronous or correlated sensory-motor experience should facilitate action imitation (Heyes & Ray, 2000). A common approach to testing the influence of experience on imitation in adults is to introduce a training stage and measure the effects of this training on imitation effects (Catmur et al., 2008; Gillmeister et al., 2008). The study reported in Chapter Three used a similar method but instead took advantage of a child's own previous experience. Children between the ages of three and seven were asked to react to an action performed by an experimenter, and were required to respond to action stimuli with both compatible and incompatible actions at different stages in the procedure. Two action sets were used for this purpose; one set incorporated actions that children often perform in synchrony (clapping and waving), and experience of synchronous performance was expected to be more limited for the other set (finger pointing and hand closing).

As predicted by the ASL approach, automatic imitation effects (i.e. the difference in time taken to react to compatible and incompatible stimuli), were greater for actions expected to be regularly performed in synchrony. Another prediction of the ASL model was also supported. Automatic imitation effects were greater for the only action that engaged two sensory modalities (clapping) in-line with the prediction that associations between multimodal sensory representations might easier facilitate an action response. The developmental trajectory of automatic imitation was also examined, but no systematic change was observed, as the ability to both imitate actions and inhibit incorrect imitative responses during incompatible trials was found to improve with age, generating a consistent automatic imitation effect (see Chapter Three, Figure 7). Together, these findings support the ASL model, and to my knowledge, this is the first study to examine predictions of an associative account of imitation in a population of this age.

Knowing that these automatic imitation effects are present in children is important. Most of the research that supports the ASL view of imitation and mirror neurons has been found in adult humans (e.g. Catmur et al., 2008; Gillmeister et al., 2008; Cook, Press, Dickinson, & Heyes, 2010), but if sensorimotor experience does facilitate imitation (Cook et al., 2014; Heyes & Ray, 2000) it is crucial that predictions of the ASL model are also supported in

children who we know have the capacity to imitate (Dean, Vale, Laland, Flynn, & Kendal, 2014; Whiten et al., 2009). If experience dependent automatic imitation effects were not identified in this population, one might conclude that existing support for the ASL view in adults may be evidence of a sensorimotor phenomenon unrelated to social learning. Furthermore, when considered with the results reported in Chapter Two of this thesis, these findings highlight the importance of considering the role of simple processes in the behaviour of humans as well as animals.

Three levels of social influence in capuchin monkeys

In Chapter Four, a study of three levels of social influence was reported. This study integrates work primarily conducted in the field of ethology into a system of social learning mechanisms developed in the field of comparative psychology. Three factors of social influence were explored. Behavioural synchrony is a measure of how coordinated a group's activity is, calculated as the probability of randomly picking two monkeys from a group and observing them perform the same behaviour (King & Cowlishaw, 2009). Surprisingly, this measure has only been used in one other study of group synchrony (King & Cowlishaw, 2009), and the study reported in Chapter Four is the first to examine this effect in New World monkeys and in a captive population. Using observational scan methods (Martin & Bateson, 2007) over a two month period

it was discovered that capuchin monkeys were more synchronous than expected by chance, and that group size and location interacted to influence this synchrony. Synchronous activity mediated by group-size might be due to the size of a group having an influencing effect on the performance of certain behaviours. The data gathered for the purpose of studying behavioural synchrony was reanalysed to examine the effects of group-size on capuchin behaviour, and larger groups predicted increased levels of vigilance, resting, foraging, and playing. The increase in the proportion of individuals being vigilant complements previous findings that suggest that in some social species vigilance may primarily serve to monitor conspecifics (Hirsch, 2002; Robinette & Ha, 2001; Treves, 1999). While the mechanism underlying group-size effects related to foraging, rest, and play is yet to be understood, it may be that a larger group-size may signal relative safety from predators or other groups and facilitate more relaxed behaviours. Indeed, when smaller groups of monkeys or individual monkeys were found in an enclosure it was much more likely that they were locomoting which is a possible indicator of unease. Certain behaviours were also found to be correlated between separate captive groups of captive monkeys after the influence of environmental factors were partialled out (e.g. weather, time of day, temperature). Behaviours related to being relaxed (e.g. foraging and play) were related between groups, as were behaviours related to being agitated (e.g. vigilance and locomotion). While it is difficult to control for every extraneous variable that might influence the

behaviour of both groups at the same point in time (e.g. number of visitors at the enclosures, unobservable activity of keeping staff) this result is in line with previous studies of the neighbour effect (Videan et al., 2005; Watson & Caldwell, 2010) where classes of behaviours related to certain motivational states (e.g. alarm calls, grooming) are associated with corresponding vocalisation from neighbouring groups.

Together, these studies of capuchin behaviour present some novel observations (e.g. this is the first evidence of behavioural synchrony and neighbour effects in capuchins). The methods used here are not new, but the use of simultaneous scan sampling facilitates many analytical possibilities. Examining these data from multiple perspectives also allows insightful observations between various levels of explanation. For example, knowing that foraging is influenced by group-size (see Table 5, Chapter Four) might explain why behavioural synchrony increases with group-size when outside where foraging is more likely to take place (see Table 2 and Table 4, Chapter Four). Furthermore, the effects examined in this chapter are underexplored in the comparative literature, possibly due to the assumption that the mechanisms thought to facilitate these group-level effects are likely indicative of social contagion or presence effects. However, these effects seem to be pervasive in the behaviour of capuchin monkeys. Social influence acts within groups, and between groups,

it is affected by sheer presence of other individuals and can generate synchronous behaviour at the group level. Observations of these effects are important, but future research efforts must explain the adaptive function of these effects, as well as the rules that mediate these processes.

Social contagion in capuchin monkeys

In Chapter Five, I aimed to investigate social contagion of behaviour and emotion. Some studies have shown that behaviour may be contagiously transmitted between neighbouring groups of conspecifics (e.g. Chapter Four, Videan et al., 2005; Watson & Caldwell, 2010), and studies of humans and other animals have found that in some cases, emotion is contagiously transmitted between individuals (measured through facial gestures Hess & Blairy, 2001; or physiological stress responses Buchanan, et al., 2012; Edgar, Lowe, Paul, & Nicol, 2011). However, little is known about the contexts under which social contagion occurs in nonhuman primates and what cognitive and emotional mechanisms might operate in these cases. It is especially important to understand the relationship between emotional contagion and behavioural contagion and the procedure employed in Chapter Five facilitated this effort. Video recordings were made of monkeys from the Living Links research site, and the content of these stimuli were chosen to represent social scenarios indicative of certain emotional states. These stimuli were presented to

conspecifics during research sessions and the behavioural and physiological responses to these stimuli were measured. A physiological or behavioural response congruent with the emotional state represented in the stimuli would be indicative of social contagion, however, no evidence of either effect was observed. Monkeys did not display an increase in stress related behaviour or salivary cortisol while watching videos of anxious individuals, and stress hormones were not suppressed by watching groupmates groom. Monkeys did however pay greater attention to videos displaying anxious conspecifics suggesting some social content was perceived by monkeys. Indeed, increased attention to stimuli of anxious groupmates might be an adaptive response to a social signal of an environmental stressor. The failure to identify either emotional or behavioural contagion was discussed in detail in Chapter Five, with specific reference to procedural limitations. While it was not possible to tease apart emotional and behaviour contagion in this particular study, the sampling of salivary cortisol and behaviour at the same time point did allow an examination of the link between physiological measures of emotional state and behavioural measures.

The collection of salivary cortisol at the beginning and end of research sessions for the purpose of examining emotional reactions to stimuli also allowed for the study of behavioural correlates of physiological stress. Unsurprisingly, a higher

rate of signalling intent to leave the research cubicle predicted an increase in cortisol, suggesting greater care should be taken in responding to this signal in future research with this study population. However, on average, monkeys' stress hormone levels did not increase over the course of research sessions. Lower levels of vigilance behaviours and lower levels of attention to stimuli were related to higher levels of average cortisol and lower scratching rates were marginally indicative of higher average cortisol. As discussed in Chapter Five, it is difficult to identify if this behavioural variation is a result of hormonal variation, or if the observed behaviours act to moderate hormone responses (Mohiyeddini et al., 2013). Research that has manipulated physiological stress through the administration of anxiolytic drugs has found that an increase in stress hormone levels leads to higher rates of self-directed behaviour (e.g. Schino, Perretta, Taglioni, Monaco, & Troisi, 1996). However, these findings cannot determine the function of scratching. The examination of emotional contagion is crucial to understand how empathic responses function in primates and other animals, but the current state of understanding is limited. Emotional contagion may not require the same level of cognitive complexity as "true empathy" (Preston & de Waal, 2002), however, it may be more important to understand this effect. While many animals may not possess the ability to take on the perspective of another individual (a prerequisite of empathy; de Waal, 2008), emotional contagion may be relatively widespread taxonomically. Emotional contagion may be adaptive in certain natural environments when

the sharing of emotional state may allow coordinated responses to potential threats, but the sharing of negative emotional states may be detrimental to animal welfare in certain captive environments. Understanding when and how these social phenomena operate may help inform practices that minimise the unnecessary sharing of emotional-state in these contexts.

Contagious scratching in capuchin monkeys

The final empirical chapter in this thesis explored the complex and compelling topic of scratching. As well as being linked to a variety of medical conditions (Ikoma et al., 2006), scratching functions to remove detritus or ectoparasites from the skin (Eckstein & Hart, 2000; Murray, 1987), is linked to anxiety in primates (Maestripieri et al., 1992; Polizzi di Sorrentino et al., 2012), and has also been found to be behaviourally contagious in humans and some nonhuman primates (Feneran et al., 2013; Holle et al., 2012). Given that rates of scratching are linked to emotional arousal, particularly anxiety (see Chapter Five; Maestripieri et al., 1992; Polizzi di Sorrentino et al., 2012; Schino, Perretta, Taglioni, & Troisi, 1996), observations of contagious scratching could be a behavioural indicator of emotional contagion. Ten capuchins were separated from their social groups and presented with two one-minute video sequences: videos of their groupmates scratching, and videos of their groupmates in neutral scenarios. Capuchin monkeys scratched more often when watching

videos of their conspecifics scratching on average, however, this effect was not significant under a more conservative analysis (see Chapter Six for more detail). No systematic differences were found in the frequency of other stress-related behaviours exhibited during the video presentations. While the results do not allow conclusive identification of scratching contagion in capuchin monkeys, the identified trend is suggestive of a contagious scratching effect. Nonetheless, a serious discussion of scratching's role as a behavioural indicator of emotion is crucial. If contagious scratching is a robust effect (as is certainly the case in humans Holle et al., 2012; Papoiu, Wang, Coghill, Chan, & Yosipovitch, 2011), this phenomenon might confound studies of emotion in primates in cases when scratching is used as a behavioural proxy. Contagious scratching, far from synchronising emotional state, may act to synchronise sensitivity to ectoparasites, which might have particular value given ectoparasites are also socially transmitted. During this study of contagions scratching, two scratching events occurring after the presentation of the scratching stimuli were observed to remove pieces of detritus from the monkey's skin. Further research will be necessary to truly understand the role of a simple scratch, and it is fitting that in this thesis on the importance of considering simpler processes, a seemingly simple behaviour is found to encourage some very serious thought.

Final comments

Throughout this thesis I have explored social learning from the bottom up with the aim of better understanding the processes involved in learning from others. Examining automatic imitation in monkeys and children has demonstrated a potential role for associative processes in action matching. Exploring the social and environmental factors that determine behaviour at the group-level, highlights the importance of conceptualising social influence as a dynamic process, better understood by considering multiple levels of explanation. We know surprisingly little about the relationship between emotion and behaviour in nonhuman animals, particularly how this relationship functions in the context of social influence. Although the current thesis has not provided extensive insights into the process of emotional contagion, some progress has been made in understanding the relationship between behaviour and physiology, an important part of developing a science of animal emotion. Finally, the consideration of contagious scratching in primates demonstrates how the study of seemingly simple effects can be worthwhile both intellectually and practically. While understanding complexity might be the primary objective of scientific enterprise, this goal can only be achieved by understanding the simple integral components. In probing human-like intelligence in other animals we may be inclined to forget the influence of simple processes on our own behaviour. When considering the evolution of advanced human cognition it is undeniably important to explore these

cognitive homologues in other animals, and this research enterprise has undoubtedly produced thought-provoking insights into the surprising complexity of animal minds. But at the same time, we must not forget our shared simplicity. As comparative scientists we must approach the study of cognition, behaviour, and emotion from both perspectives, from the bottom up as well as from the top down. In doing so, we will better understand not only the nature of complex processes in human behaviour, but the fundamental role of simple mechanisms.

References

Aiello, J. R., & Douthitt, E. A. (2001). Social facilitation from Triplett to
electronic performance monitoring. *Group Dynamics: Theory, Research, and
Practice*, *5*, 163–180.

Akins, C. K., & Zentall, T. R. (1996). Imitative learning in male Japanese quail
(*Coturnix japonica*) using the two-action method. *Journal of Comparative
Psychology*, *110*, 316–320.

Amici, F., Aureli, F., & Call, J. (2013). Response facilitation in the four great
apes: is there a role for empathy? *Primates*, *55*, 113-118

Anderson, J. R. (2010). Non-human primates: a comparative developmental
perspective on yawning. *Frontiers of Neurology and Neuroscience*, *28*, 63–76.

Anderson, J. R., Kuroshima, H., & Fujita, K. (2010). Delay of gratification in
capuchin monkeys (*Cebus apella*) and squirrel monkeys (*Saimiri sciureus*).
Journal of Comparative Psychology, *124*, 205–210.

Anderson, J. R., Kuroshima, H., Paukner, A., & Fujita, K. (2009). Capuchin
monkeys (*Cebus apella*) respond to video images of themselves. *Animal
Cognition*, *12*, 55–62.

253

Anderson, J. R., Myowa-Yamakoshi, M., & Matsuzawa, T. (2004). Contagious yawning in chimpanzees. *Biology Letters*, *271*, S468–S470.

Andreassi, J. L., & Greco, J. R. (1975). Etlects of bisensory stimulation on reaction time and the evoked cortical potential. *Physiological Psychology*, *3*, 189–194.

Andrew, D., & Craig, A. D. (2001). Spinothalamic lamina I neurons selectively sensitive to histamine: a central neural pathway for itch. *Nature Neuroscience*, *4*, 72–77.

Andrew, R. J. (1956). Some remarks on behaviour in conflict situations, with special reference to *Emberiza Spp*. *The British Journal of Animal Behaviour*, *4*, 41–45.

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

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

Anselme, P. (2008). Abnormal patterns of displacement activities: A review and reinterpretation. *Behavioural Processes*, *79*, 48–58.

Arck, P. C., Slominski, A., Theoharides, T. C., Peters, E. M. J., & Paus, R. (2006). Neuroimmunology of stress: skin takes center stage. *The Journal of Investigative Dermatology*, *126*, 1697–704.

Ash, H. (2014). Assessing the welfare of laboratory-housed marmosets (*Callithrix jacchus*): Effects of breeding and infant rearing background (Unpublished doctoral thesis). University of Stirling, Scotland.

Aureli, F., & van Schaik, C. P. (1991). Post-conflict behaviour in long-tailed macaques (*Macaca fascicularis*): II. Coping with the uncertainty. *Ethology*, *89*, 101–114.

Avarguès-Weber, A., & Chittka, L. (2014). Local enhancement or stimulus enhancement? Bumblebee social learning results in a specific pattern of flower preference. *Animal Behaviour*, *97*, 185–191.

Baker, K., & Aureli, F. (1996). The neighbor effect : Other groups influence intragroup agonistic behavior in captive chimpanzees. *American Journal of Primatology*, *40*, 281–291.

Bard, K. A. (2007). Neonatal imitation in chimpanzees (*Pan troglodytes*) tested with two paradigms. *Animal Cognition*, *10*, 233–242.

Bargh, J., & Chartrand, T. L. (1999). The unbearable automaticity of being. *American Psychologist*, *54*, 462–479.

Barrett, L. (2011a). *Beyond the brain: How body and environment shape animal and human minds*. Princeton, NJ: Princeton University Press.

Barrett, L. (2011b). Why Behaviorism isn't Satanism. In J. Vonk & T. Shackelford (Eds.), *The Oxford history of comparative evolutionary psychology* (pp. 17-38). New York: Oxford University Press.

Barrett, L., Henzi, P., & Rendall, D. (2007). Social brains, simple minds: does social complexity really require cognitive complexity? *Philosophical Transactions of the Royal Society of London: B,362*, 561–575.

Barros, M., Boere, V., Huston, J., & Tomaz, C. (2000). Measuring fear and anxiety in the marmoset (*Callithrix penicillata*) with a novel predator confrontation model: effects of diazepam. *Behavioural Brain Research, 108*, 205–211.

Bates, D., Maechler, M., Bolker B., & Walker, S. (2015). *lme4: Linear mixed-effects models using Eigen and S4*. In: R package version 1.1-9. https://CRAN.R-project.org/package=lme4.

Beauchamp, G. (2009). Sleeping gulls monitor the vigilance behaviour of their neighbours. *Biology Letters, 5*, 9–11.

Beauchamp, G. (2012). Flock size and density influence speed of escape waves in semipalmated sandpipers. *Animal Behaviour, 83*, 1125–1129.

Beauchamp, G. (2013). Social foragers adopt a riskier foraging mode in the centre of their groups. *Biology Letters*, *9*, 20130528.

Bekkering, H., & Wohlschlager, A. (2000). Imitation of gestures in children is goal-directed. *The Quarterly Journal of Experimental Psychology*, 53, 153–164.

Ben-Ami Bartal, I., Decety, J., & Mason, P. (2011). Empathy and pro-social behavior in rats. *Science, 334,* 1427–1430.

Beran, M. J., Klein, E. D., Evans, T. A, Chan, B., Flemming, T. M., Harris, E. H., … Rumbaugh, D. M. (2008). Discrimination reversal learning in capuchin monkeys (*Cebus apella*). *The Psychological Record*, *58*, 3–14.

Berdahl, A., Torney, C. J., Ioannou, C. C., Faria, J. J., & Couzin, I. D. (2013). Emergent sensing of complex environments by mobile animal groups. *Science*, *339*, 574–576.

Bergum, B. O., & Lehr, D. J. (1963). Effects of authoritarianism on vigilance performance. *Journal of Applied Psychology*, *47*, 75–77.

Bindra, D. (1959). An interpretation of the displacement phenomonon. *British Journal of Psychology*, *50*, 263–268.

Blanchard, R. J., Flannelly, K. J., & Blanchard, D. C. (1986). Defensive behavior of laboratory and wild *Rattus norvegicus*. *Journal of Comparative Psychology*, *100,* 101–107.

Bond, A. B., Kamil, A. C., & Balda, R. P. (2007). Serial reversal learning and the evolution of behavioral flexibility in three species of North American corvids (*Gymnorhinus cyanocephalus, Nucifraga columbiana, Aphelocoma californica*). *Journal of Comparative Psychology*, *121*, 372–379.

Bonini, L., & Ferrari, P. F. (2011). Evolution of mirror systems: a simple mechanism for complex cognitive functions. *Annals of the New York Academy of Sciences*, *1225*, 166–175.

Bourgeois, P., & Hess, U. (2008). The impact of social context on mimicry. *Biological Psychology*, *77*, 343–352.

Bowman, N. D., Weber, R., Tamborini, R., & Sherry, J. L. (2013). Facilitating game play: How others affect performance at and enjoyment of video games. *Media Psychology*, *16*, 39-64.

Boyer, T. W., Longo, M. R., & Bertenthal, B. I. (2012). Is automatic imitation a specialized form of stimulus-response compatibility? Dissociating imitative and spatial compatibilities. *Acta Psychologica*, *139*, 440–448.

Brass, M., Bekkering, H., & Prinz, W. (2001). Movement observation affects movement execution in a simple response task. *Acta Psychologica*, *106*, 3–22.

Brass, M., Bekkering, H., Wohlschläger, A., & Prinz, W. (2000). Compatibility between observed and executed finger movements: comparing symbolic, spatial, and imitative cues. *Brain and Cognition, 44*, 124–43.

Brass, M., & Heyes, C. (2005). Imitation: is cognitive neuroscience solving the correspondence problem? *Trends in Cognitive Sciences, 9*, 489–495.

Brass, M. & Muhle-Karbe, P. S. (2013). More than associations: An ideomotor perspective on mirror neurons. *Behavioral and Brain Sciences,37*,195-196.

Buchanan, T. W., Bagley, S., Stansfield, R., & Preston, S. D. (2012). The Empathic, Physiological Resonance of Stress. *Social Neuroscience*, *7*, 191–201.

Buttelmann, D., Carpenter, M., Call, J., & Tomasello, M. (2007). Enculturated chimpanzees imitate rationally. *Developmental Science*, *10*, 1688-1705.

Byrne, R. W. (1994). The evolution of intelligence. In P. J. B. Slater & T. R. Halliday (Eds.), *Behaviour and Evolution* (pp. 223–265). Cambridge: Cambridge University Press.

Byrne, R. W. (2002a). Emulation in apes: verdict "not proven". *Developmental Science*, *5*, 20–22.

Byrne, R. W. (2002b). Imitation of novel complex actions: What does the evidence from animals mean? *Advances in the Study of Behavior*, *31*, 77–104.

Byrne, R. W., & Russon, A. E. (1998). Learning by imitation: A hierarchical approach. *The Behavioral and Brain Sciences*, *21*, 667–721.

Caggiano, V., Fogassi, L., Rizzolatti, G., & Thiery, P. (2009). Mirror neurons differentially encode the peripersonal and extrapersonal space of monkeys. *Science*, *324*, 403–406.

Caldwell, C. A., & Millen, A. E. (2009). Social learning mechanisms and cumulative cultural evolution. Is imitation necessary? *Psychological Science*, *20*, 1478–1483.

Caldwell, C. A., & Whiten, A. (2002). Evolutionary perspectives on imitation : is a comparative psychology of social learning possible ? *Animal Cognition*, *5*, 193–208.

Caldwell, C. A., & Whiten, A. (2004). Testing for social learning and imitation in common marmosets, *Callithrix jacchus*, using an artificial fruit. *Animal Cognition*, *7*, 77–85.

Call, J. (2001). Body imitation in an enculturate orangutan (*Pongo pygmaeus*). *Cybernetics and Systems: An International Journal*, *32*, 97–119.

Call, J., & Carpenter, M. (2002). Three sources of information in social learning. In K. Dautenhahn & C. L. Nehaniv (Eds.), *Imitation in animals and artifacts* (pp. 211–228). Cambridge, MA: MIT Press.

Campbell, M. W., & de Waal, F. B. M. (2011). Ingroup-outgroup bias in

contagious yawning by chimpanzees supports link to empathy. *PloS One*,

6, e18283.

Capa, R. L., Marshall, P. J., Shipley, T. F., Salesse, R. N., & Bouquet, C. A. (2011).

Does motor interference arise from mirror system activation? The effect of

prior visuo-motor practice on automatic imitation. *Psychological Research*,

75, 152–7.

Carder, G., & Semple, S. (2008). Visitor effects on anxiety in two captive groups

of western lowland gorillas. *Applied Animal Behaviour Science, 115*, 211–220.

Carere, C., Montanino, S., Moreschini, F., Zoratto, F., Chiarotti, F., Santucci, D.,

& Alleva, E. (2009). Aerial flocking patterns of wintering starlings, Sturnus

vulgaris, under different predation risk. *Animal Behaviour, 77*, 101–107.

Castles, D., Whiten, A., & Aureli, F. (1999). Social anxiety, relationships and

self-directed behaviour among wild female olive baboons. *Animal

Behaviour, 58*, 1207–1215.

Catmur, C. (2011). Contingency is crucial for creating imitative responses.

Frontiers in Human Neuroscience, 5, 1-2.

Catmur, C., Gillmeister, H., Bird, G., Liepelt, R., Brass, M., & Heyes, C. (2008).

Through the looking glass: Counter-mirror activation following

incompatible sensorimotor learning. *The European Journal of Neuroscience*, *28*, 1208–1215.

Catmur, C., & Heyes, C. (2011). Time course analyses confirm independence of imitative and spatial compatibility. *Journal of Experimental Psychology: Human Perception and Performance*, *37*, 409–421.

Catmur, C., Mars, R. B., Rushworth, M. F., & Heyes, C. (2011). Making Mirrors: Premotor cortex stimulation enhances mirror and counter-mirror motor facilitation. *Journal of Cognitive Neuroscience*, *23*, 2352–2362.

Catmur, C., Walsh, V., & Heyes, C. (2007). Sensorimotor learning configures the human mirror system. *Current Biology*, *17*, 1527–1531.

Catmur, C., Walsh, V., & Heyes, C. (2009). Associative sequence learning: The role of experience in the development of imitation and the mirror system. *Philosophical Transactions of the Royal Society of London: B.*, *364*, 2369–80.

Chan, S., & Debono, M. (2010). Replication of cortisol circadian rhythm: New advances in hydrocortisone replacement therapy. *Therapeutic Advances in Endocrinology and Metabolism*, *1*, 129–138.

Chapman, T. L., Holcomb, M. P., Spivey, K. L., Sehr, E. K., & Gall, B. G. (2015). A test of local enhancement in amphibians. *Ethology*, *121*, 308–314.

Chartrand, T. L., & Bargh, J. A. (1999). The chameleon effect: the perception-behaviour link and social interaction. *Journal of Personality and Social Psychology*, *76*, 893–910.

Cilia, J., & Piper, D. (1997). Marmoset conspecific confrontation: an ethologically-based model of anxiety. *Pharmacology Biochemistry and Behavior*, *58*, 85–91.

Cohen, J. (1992). A Power Primer. *Psychological Bulletin*, *112*, 155-159.

Cohen, J. A., & Price, E. O. (1979). Grooming in the Norway rat: Displacement activity or "boundary-shift"? *Behavioral and Neural Biology*, *26*, 177–188.

Cook, R. (2012). The ontogenetic origins of mirror neurons: Evidence from "tool-use" and "audiovisual" mirror neurons. *Biology Letters*, *8*, 856-859.

Cook, R., Bird, G., Catmur, C., Press, C., & Heyes, C. (2014). Mirror neurons: From origin to function. *Behavioral and Brain Sciences*, *37*, 177–192.

Cook, R., Dickinson, A., & Heyes, C. (2012). Contextual modulation of mirror and countermirror sensorimotor associations. *Journal of Experimental Psychology: General*, 141, 774-787.

Cook, R., Press, C., Dickinson, A., & Heyes, C. (2010). Acquisition of automatic imitation is sensitive to sensorimotor contingency. *Journal of Experimental Psychology: Human Perception and Performance, 36*, 840–52.

Couzin, I. D. (2007). Collective minds. *Nature*, *445*, 715.

Couzin, I. D., Krause, J., James, R., Ruxton, G. D., & Franks, N. R. (2002).

Collective memory and spatial sorting in animal groups. *Journal of*

Theoretical Biology, *218*, 1–11.

Custance, D., Whiten, A., & Bard, K. (1995). Can young chimpanzees (*Pan*

troglodytes) imitate arbitrary actions? Hayes & Hayes (1952) revisited.

Behaviour, *132*, 837–859.

Custance, D., Whiten, A., & Fredman, T. (1999). Social learning of an artificial

fruit task in capuchin monkeys (*Cebus apella*). *Journal of Comparative*

Psychology, *113*, 13–23.

D'Eath, R. B. (1998). Can video images imitate real stimuli in animal behaviour

experiments? *Biological Reviews*, *73*, 267–292.

Damasio, A. (1996). The somatic marker hypothesis and the possible functions

of the prefrontal cortex. *Philosophical Transactions of the Royal Society of*

London: B., *351*, 1413–1420.

Daniel, J. R., Santos, A. J., & Vicente, L. (2008). Correlates of self-directed

behaviors in captive C*ercopithecus aethiops*. *International Journal of*

Primatology, *29*, 1219–1226.

Davidson, S., & Giesler, G. (2010). The multiple pathways for itch and their interactions with pain. *Trends in Neurosciences*, *33*, 550–558.

Davidson, S., Zhang, X., Khasabov, S. G., Moser, H. R., Honda, C. N., Simone, D. A, & Giesler, G. J. (2012). Pruriceptive spinothalamic tract neurons: Physiological properties and projection targets in the primate. *Journal of Neurophysiology*, *108*, 1711–23.

Davidson, S., Zhang, X., Yoon, C. H., Khasabov, S. G., Simone, D. A, & Giesler, G. J. (2007). The itch-producing agents histamine and cowhage activate separate populations of primate spinothalamic tract neurons. *The Journal of Neuroscience*, *27*, 10007–10014.

Davila-Ross, M., Allcock, B., Thomas, C., & Bard, K. a. (2011). Aping expressions? Chimpanzees produce distinct laugh types when responding to laughter of others. *Emotion*, *11*, 1013–1020.

Davila-Ross, M., Menzler, S., & Zimmermann, E. (2008). Rapid facial mimicry in orangutan play. *Biology Letters*, *4*, 27–30.

Dawson, E. H., Avarguès-Weber, A., Chittka, L., & Leadbeater, E. (2013). Learning by observation emerges from simple associations in an insect model. *Current Biology*, *23*, 727–730.

265

Dawson, E. H., & Chittka, L. (2014). Bumblebees (*Bombus terrestris*) use social information as an indicator of safety in dangerous environments. *Proceedings of the Royal Society of London: B, 281*, 20133174.

Dawson, B. V, & Foss, B. M. (1965). Observational learning in budgerigars. *Animal Behaviour*, *13*, 470–474.

De Klerk, C. C. J. M., Johnson, M. H., Heyes, C. M., & Southgate, V. (2014). Baby steps: Investigating the development of perceptual-motor couplings in infancy. *Developmental Science*, *2*, 270–280.

De Waal, F. B. M. (2008). Putting the altruism back into altruism: the evolution of empathy. *Annual Review of Psychology*, *59*, 279–300.

De Waal, F. B. M., & Ferrari, P. F. (2010). Towards a bottom-up perspective on animal and human cognition. *Trends in Cognitive Sciences*, *14*, 201–207.

Dean, L. G., Vale, G. L., Laland, K. N., Flynn, E., & Kendal, R. L. (2014). Human cumulative culture: a comparative perspective. *Biological Reviews of the Cambridge Philosophical Society*, *89*, 284–301.

Decastro, J. M. (1994). Family and friends produce greater social facilitation of food-intake than other companions. *Physiology and Behavior*, *56*, 445–455.

Decety, J., & Meyer, M. (2008). From emotion resonance to empathic understanding: a social developmental neuroscience account. *Development and Psychopathology*, *20*, 1053–1080.

Decety, J., Norman, G. J., Berntson, G. G., & Cacioppo, J. T. (2012). A neurobehavioral evolutionary perspective on the mechanisms underlying empathy. *Progress in Neurobiology*, *98*, 38–48.

Del Giudice, M., Manera, V., & Keysers, C. (2009). Programmed to learn? The ontogeny of mirror neurons. *Developmental Science*, *12*, 350–363.

Delius, J. (1967). Displacement activities and arousal. *Nature*, *214*, 1259–1260.

Dennett, D. C. (1983). Intentional systems in cognitive ethology: The "Panglossian paradigm" defended. *Behavioral and Brain Sciences*, *6*, 343.

Dezecache, G., Conty, L., Chadwick, M., Philip, L., Soussignan, R., Sperber, D., & Grèzes, J. (2013). Evidence for unintentional emotional contagion beyond dyads. *PloS One*, *8*, e67371.

Di Pellegrino, G., Fadiga, L., Fogassi, L., Gallese, V., & Rizzolatti, G. (1992). Understanding motor events: a neurophysiological study. *Experimental Brain Research*, *91*, 176–180.

Dickerson, K., Gerhardstein, P., Zack, E., & Barr, R. (2008). Age-related changes in learning across early childhood: A new imitation task. *Developmental Psychobiology, 55*, 719-732.

Dickerson, S. S., & Kemeny, M. E. (2004). Acute stressors and cortisol responses: A theoretical integration and synthesis of laboratory research. *Psychological Bulletin, 130*, 355–391.

Diezinger, F., & Anderson, J. R. (1986). Starting from scratch: A first look at a "displacement activity" in group-living rhesus monkeys. *American Journal of Primatology, 11*, 117–124.

Dindo, M., Thierry, B., & Whiten, A. (2008). Social diffusion of novel foraging methods in brown capuchin monkeys (*Cebus apella*). *Proceedings of the Royal Society of London: B., 275*, 187–193.

Dindo, M., Whiten, A., & de Waal, F. B. M. (2009a). In-group conformity sustains different foraging traditions in capuchin monkeys (*Cebus apella*). *PloS One, 4*, e7858.

Dindo, M., Whiten, A., & de Waal, F. B. M. (2009b). Social facilitation of exploratory foraging behavior in capuchin monkeys (*Cebus apella*). *American Journal of Primatology, 71*, 419–26.

Ebensperger, L., Hurtado, M., & Ramos-Jiliberto, R. (2006). Vigilance and collective detection of predators in degus (*Octodon degus*). *Ethology*, *112*, 879-887.

Eckstein, R., & Hart, B. (2000). Grooming and control of fleas in cats. *Applied Animal Behaviour Science*, *68*, 141–150.

Edgar, J. L., Lowe, J. C., Paul, E. S., & Nicol, C. J. (2011). Avian maternal response to chick distress. *Proceedings of the Royal Society of London: B.*, *278*, 3129–3134.

Edgar, J. L., Paul, E. S., Harris, L., Penturn, S., & Nicol, C. J. (2012). No evidence for emotional empathy in chickens observing familiar adult conspecifics. *PLoS One*, *7*, e31542.

Ekman, P., Levenson, R. W., & Friesen, W. V. (1983). Autonomic nervous system activity distinguishes among emotions. *Science*, *221*, 1208–1210.

Engel, J., & Lamprecht, J. (1997). Doing what everybody does? A procedure for investigating behavioural synchronization. *Journal of Theoretical Biology*, *185*, 255–62.

Fagot, J., Gullstrand, J., Kemp, C., Defilles, C., & Mekaouche, M. (2013). Effects of freely accessible computerized test systems on the spontaneous

behaviors and stress level of Guinea baboons (*Papio papio*). *American Journal of Primatology*, *9*, 56-64.

Fairbanks, L. A., Mcguire, M. T., & Candace, J. H. (1982). Nonverbal interaction of patients and therapists during psychiatric interviews. *Journal of Abnormal Psychology*, *91,* 109–119.

Faria, J. J., Dyer, J. R. G., Clément, R. O., Couzin, I. D., Holt, N., Ward, A. J. W., … Krause, J. (2010). A novel method for investigating the collective behaviour of fish: Introducing "Robofish." *Behavioral Ecology and Sociobiology*, *64*, 1211–1218.

Feldman, J. M., & Albuquerque, M. (1968). Successive discrimination reversal performance, *13*, 265–266.

Feneran, A. N., O'Donnell, R., Press, A., Yosipovitch, G., Cline, M., Dugan, G., … Shively, C. a. (2013). Monkey see, monkey do: Contagious itch in nonhuman primates. *Acta Dermato-Venereologica*, *93*, 27–9.

Ferrari, P. F., Visalberghi, E., Paukner, A., Fogassi, L., Ruggiero, A., & Suomi, S. J. (2006). Neonatal imitation in rhesus macaques. *PLoS Biology*, *4*, e302.

Fichtel, C., Pyritz, L., & Kappeler, P. M. (2011). Coordination of group movements in non-human primates. In M. Boos, M. Kolbe, S. Ellwart, & P.

M. Kappeler (Eds.), *Coordination in human and non-human primate groups* (pp. 37–56). Heidelberg: Springer

Field, A. P. (2013). *Discovering statistics using IBM SPSS Statistics: and sex and drugs and rock 'n' roll (fourth edition)*. London: Sage publications.

Field, T. M., Woodson, R., Greenberg, R., & Cohen, D. (1982). Discrimination and imitation of facial expression by neonates. *Science, 218*, 179–181.

Flynn, V., Masur, E. F., & Eichorst, D. L. (2004). Opportunity versus disposition as predictors of infants' and mothers' verbal and action imitation. *Infant Behavior and Development, 27*, 303–314.

Fontaine, R. (1984). Imitative skills between birth and six months. *Infant Behavior and Development, 7*, 323–333.

Fragaszy, D. M., Deputte, B., Cooper, E. J., Colbert-White, E. N., & Hémery, C. (2011). When and how well can human-socialized capuchins match actions demonstrated by a familiar human? *American Journal of Primatology, 73*, 643–654.

Fragaszy, D. M., Feuerstein, J. M., & Mitra, D. (1997). Transfers of food from adults to infants in tufted capuchins (*Cebus apella*). *Journal of Comparative Psychology, 111*, 194–200.

Fragaszy, D. M., & Visalberghi, E. (1989). Social influences on the acquisition of tool-using behaviors in tufted capuchin monkeys (*Cebus apella*). *Journal of Comparative Psychology*, *103*, 159–170.

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

Fraser, O. N., & Bugnyar, T. (2010). Do ravens show consolation? Responses to distressed others. *PloS One*, *5*, e10605.

Fraser, O. N., Stahl, D., & Aureli, F. (2008). Stress reduction through consolation in chimpanzees. *Proceedings of the National Academy of Sciences of the United States of America*, *105*, 8557–8562.

Frederick, S., Loewenstein, G., & O'Donoghue, T. (2002). Time discounting and time preference: A critical review. *Journal of Economic Literature*, *40*, 351–401.

Frith, C., & Frith, U. (2008). Implicit and explicit processes in social cognition. *Neuron*, *60*, 503–10.

Fuhrmann, D., Ravignani, A., Marshall-Pescini, S., & Whiten, A. (2014). Synchrony and motor mimicking in chimpanzee observational learning. *Scientific Reports*, *4*, 5283.

Fujii, N., Hihara, S., & Iriki, A. (2007). Dynamic social adaptation of motion-related neurons in primate parietal cortex. *PLoS One, 2,* e397

Fukuoka, M., Miyachi, Y., & Ikoma, A. (2013). Mechanically evoked itch in humans. *Pain*, *154*, 897–904.

Galef, B. G. (1988). Imitation in animals: History, definition, and interpretation of data from the Psychological lab. In T. R. Zentall & B. G. Galef (Eds.), *Social Learning: Psychological and Biological Perspectives* (pp. 3–27). Hillsdale, NJ: Erlbaum.

Galef, B. G. (1993). Functions of social learning about food: A causal analysis of effects of diet novelty on preference transmission. *Animal Behaviour*, *46*, 257–265.

Galef, B. G. (2013). Imitation and local enhancement: Detrimental effects of consensus definitions on analyses of social learning in animals. *Behavioural Processes*, *100*, 123–130.

Gallese, V., Fadiga, L., Fogassi, L., & Rizzolatti, G. (1996). Action recognition in the premotor cortex. *Brain*, *119*, 593–609.

Gallese, V., Gernsbacher, M. A., Heyes, C., Hickok, G., & Iacoboni, M. (2011). Mirror neuron forum. *Perspectives on Psychological Science*, *6*, 369–407.

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, A. C. (2011). Why do we yawn? Primitive versus derived features. *Neuroscience and Biobehavioral Reviews*, *35*, 765–9.

Galton, F. (1907). Vox populi. *Nature*, *75*, 450–451.

Garcia-Marques, T., Fernandes, A., Fonseca, R., & Prada, M. (2015). Social presence and the composite face effect. *Acta Psychologica*, *158*, 61–66.

Gazzola, V., & Keysers, C. (2009). The observation and execution of actions share motor and somatosensory voxels in all tested subjects: single-subject analyses of unsmoothed fMRI data. *Cerebral Cortex*, *19*, 1239–55.

Gerstadt, C. L., Hong, Y. J., & Diamond, A. (1994). The relationship between cognition and action: Performance of children 3 1/2-7 years old on a Stroop-like day-night test. *Cognition*, *53*, 129–153.

Gibson, J. J. (1977). The theory of affordances. In Shaw, R., & Bransford, J., (Eds.), *Perceiving, acting, and knowing: Toward an ecological psychology*. Hillsdale, NJ: Lawrence Erlbaum Associates.

Gillmeister, H., Catmur, C., Liepelt, R., Brass, M., & Heyes, C. (2008). Experience-based priming of body parts: a study of action imitation. *Brain Research*, *1217*, 157–170.

Grand, A., & Leighty, K. (2013). The neighbor effect in bachelor and breeding groups of western lowland gorillas (*Gorilla gorilla gorilla*). *International Journal of Comparative Psychology*, *26*, 26-36.

Guillette, L. M., & Healy, S. D. (2014). Mechanisms of copying behaviour in zebra finches. *Behavioural Processes*, *108*, 177-182.

Hari, R., Forss, N., Avikainen, S., Kirveskari, E., Salenius, S., & Rizzolatti, G. (1998). Activation of human primary motor cortex during action observation: a neuromagnetic study. *Proceedings of the National Academy of Sciences of the United States of America*, *95*, 15061–5.

Harlow, H. F. (1932). Social facilitation of feeding in the albino rat. *Journal of Genetic Psychology*, *41*, 211–221.

Harr, A. L., Gilbert, V. R., & Phillips, K. a. (2009). Do dogs (*Canis familiaris*) show contagious yawning? *Animal Cognition*, *12*, 833–837.

Hatfield, E., Rapson, R., & Le, Y. L. (2009). Primitive emotional contagion: Recent research. In J. Decety & W. Ickes (Eds.), *The Social Neuroscience of Empathy*. Cambridge, MA: MIT Press

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

Hayes, L. A., & Watson, J. S. (1981). Neonatal Imitation : Fact or Artifact ? *Developmental Psychology*, *17*, 655–660.

Heimann, M., Nelson, K., & Schaller, J. (1989). Neonatal imitation of tongue protrusion and mouth opening: Methodological aspects and evidence of early individual differences. *Scandinavian Journal of Psychology*, *30*, 90–101.

Heintz, M. R., Santymire, R. M., Parr, L. a., & Lonsdorf, E. V. (2011). Validation of a cortisol enzyme immunoassay and characterization of salivary cortisol circadian rhythm in chimpanzees (*Pan troglodytes*). *American Journal of Primatology*, *73*, 903–908.

Helbing, D., Buzna, L., Johansson, a, & Werner, T. (2005). Self-organized pedestrian crowd dynamics: Experiments, simulations, and design solutions. *Transportation Science*, *39*, 1–24.

Hershenson, M. (1962). Reaction time as a measure of intersensory facilitation. *Journal of Experimental Psychology*, *63*, 289–293.

Hess, U., & Blairy, S. (2001). Facial mimicry and emotional contagion to dynamic emotional facial expressions and their influence on decoding accuracy. *International Journal of Psychophysiology*, *40*, 129–41.

Heyes, C. (1993). Imitation, culture and cognition. *Animal Behaviour*, *46*, 999–1010.

Heyes, C. (1994). Socal learning in animals: Categories and mechanisms. *Biology Review*, *69*, 207–231.

Heyes, C. (2005). Imitation by association. In S. Hurley & N. Chater (Eds.), *Perspectives on imitation: From cognitive neuroscience to social science* (Vol 1., pp. 157–176). Cambridge, MA: MIT Press.

Heyes, C. (2010). Where do mirror neurons come from? *Neuroscience and Biobehavioral Reviews*, *34*, 575–83.

Heyes, C. (2011). Automatic imitation. *Psychological Bulletin*, *137*, 463–83.

Heyes, C. (2012a). Simple minds: A qualified defence of associative learning. *Philosophical Transactions of the Royal Societyof London: B*, *367*, 2698–2703.

Heyes, C. (2012b). What's social about social learning? *Journal of Comparative Psychology*, *126*, 193–202.

Heyes, C. (2013). Imitation: Associative and Context Dependent. In W. Prinz, M. Beisert, & A. Herwig (Eds.), *Action Science: Foundations of An Emerging Discipline* (pp. 309–332). Cambridge, MA: MIT Press.

Heyes, C., Bird, G., Johnson, H., & Haggard, P. (2005). Experience modulates automatic imitation. *Cognitive Brain Research*, *22*, 233–40.

Heyes, C., & Dawson, G. (1990). A demonstration of observational learning in rats using a bidirectional control. *The Quarterly Journal of Experimental Psychological Biology, 42B*, 59–71.

Heyes, C., & Ray, E. (2000). What is the significance of imitation in animals? *Advances in the Study of Behavior*, *29*, 215–245.

Heyes, C., Ray, E. D., Mitchell, C. J., & Nokes, T. (2000). Stimulus enhancement: Controls for social facilitation and local enhancement. *Learning and Motivation*, *31*, 83–98.

Hirsch, B. T. (2002). Social monitoring and vigilance behavior in brown capuchin monkeys (*Cebus apella*). *Behavioral Ecology and Sociobiology*, *52*, 458–464.

Holle, H., Warne, K., Seth, A. K., Critchley, H. D., & Ward, J. (2012). Neural basis of contagious itch and why some people are more prone to it. *Proceedings of the National Academy of Sciences of the United States of America*, *109*, 19816–19821.

Hopper, L. M. (2010). "Ghost" experiments and the dissection of social learning in humans and animals. *Biological Reviews of the Cambridge Philosophical Society*, *85*, 685–701.

Hopper, L. M., Lambeth, S. P., Schapiro, S. J., & Whiten, A. (2008). Observational learning in chimpanzees and children studied through "ghost" conditions. *Proceedings of the Royal Society of London: B,275*, 835–840.

Hoppitt, W., Blackburn, L., & Laland, K. N. (2007). Response facilitation in the domestic fowl. *Animal Behaviour*, *73*, 229–238.

Hoppitt, W., & Laland, K. (2008a). Social processes influencing learning in animals: a review of the evidence. *Advances in the Study of Behavior*, *38,* 105–165.

Hoppitt, W., & Laland, K. N. (2008b). Social processes affecting feeding and drinking in the domestic fowl. *Animal Behaviour*, *76*, 1529–1543.

Hoppitt, W., & Laland, K. N. (2013). *Social Learning: An Introduction to Mechanisms, Methods, and Models*. Princeton, NJ: Princeton University Press.

Horner, V., & Whiten, A. (2005). Causal knowledge and imitation/emulation switching in chimpanzees (*Pan troglodytes*) and children (*Homo sapiens*). *Animal Cognition*, *8*, 164–181.

Hosey, G., R. (2000). Zoo animals and their human audiences: What is the visitor effect? *Animal Welfare*, *9*, 343–357.

Huber, L., Rechberger, S., & Taborsky, M. (2001). Social learning affects object exploration and manipulation in keas, *Nestor notabilis*. *Animal Behaviour*, *62*, 945–954.

Huxley, J. (1914). The courtship habits of the great crested grebe (*Podiceps cristatus*); with an addition to the theory of sexual selection. *Proceedings of the Zoological Society of London*, *84*, 491–562.

Iacoboni, M. (2009). Imitation, empathy, and mirror neurons. *Annual Review of Psychology*, *60*, 653–70.

Iacoboni, M., Woods, R. P., Brass, M., Bekkering, H., Mazziotta, J. C., & Rizzolatti, G. (1999). Cortical Mechanisms of Human Imitation. *Science*, *286*, 2526–2528.

Ikoma, A., Handwerker, H., Miyachi, Y., & Schmelz, M. (2005). Electrically evoked itch in humans. *Pain*, *113*, 148–154.

Ikoma, A., Steinhoff, M., Ständer, S., Yosipovitch, G., & Schmelz, M. (2006). The neurobiology of itch. *Nature Reviews. Neuroscience*, *7*, 535–547.

Jacobson, S. W. (1979). Matching behavior in the young infant. *Child Development*, *50*, 425–430.

Jacobson, S. W., & Kagan, J. (1969). Interpreting "imative" responses in early

infancy. *Science*, *205*, 115–117.

Janssen, S. A. (2002). Negative affect and sensitization to pain. *Scandinavian

Journal of Psychology*, *43*, 131–137.

Joëls, M., Karst, H., Alfarez, D., Heine, V. M., Qin, Y., van Riel, E., … Krugers,

H. J. (2004). Effects of chronic stress on structure and cell function in rat

hippocampus and hypothalamus. *Stress, 7*, 221–231.

Joly-Mascheroni, R. M., Senju, A., & Shepherd, A. J. (2008). Dogs catch human

yawns. *Biology Letters*, *4*, 446–448.

Jones, S. S. (2006). Infants learn to imitate by being imitated. In *Fifth proceedings

of the international conference of development and learning*.

Jones, S. S. (1996). Imitation or exploration? Young infants' matching of adults'

oral gestures. *Child Development*, *67*, 1952–1969.

Jones, S. S. (2006). Exploration or imitation? The effect of music on 4-week-old

infants' tongue protrusions. *Infant Behavior & Development*, *29*, 126–130.

Jones, S. S. (2007). Imitation in infancy: the development of mimicry.

Psychological Science, *18*, 593–599.

Jones, S. S. (2009). The development of imitation in infancy. *Philosophical Transactions of the Royal Society of London: B*, *364*, 2325–2335.

Jutel, M., Watanabe, T., Akdis, M., Blaser, K., & Akdis, C. (2002). Immune regulation by histamine. *Current Opinion in Immunology*, *14*, 735–740.

Kahneman, D. (2011). *Thinking, Fast and Slow*. New York: Farrar, Straus and Giroux.

Katz, R. J., Roth, K. A., & Carroll, B. J. (1981). Acute and chronic stress effects on open field activity in the rat: implications for a model of depression. *Neuroscience and Biobehavioral Reviews, 5*, 247–251.

Keysers, C., Kohler, E., Umiltà, M. A, Nanetti, L., Fogassi, L., & Gallese, V. (2003). Audiovisual mirror neurons and action recognition. *Experimental Brain Research*, *153*, 628–636.

Keysers, C., & Perrett, D. I. (2004). Demystifying social cognition: A Hebbian perspective. *Trends in Cognitive Sciences*, *8*, 501–507.

Kilner, J. M., & Lemon, R. N. (2013). What we know currently about mirror neurons. *Current Biology*, *23*, R1057–R1062.

King, A. J., & Cowlishaw, G. (2009). All together now: Behavioural synchrony in baboons. *Animal Behaviour*, *78*, 1381–1387.

King, A. J., Sueur, C., Huchard, E., & Cowlishaw, G. (2011). A rule-of-thumb based on social affiliation explains collective movements in desert baboons. *Animal Behaviour*, *82*, 1337–1345.

Kokkinaki, T., & Kugiumutzakis, G. (2000). Basic aspects of vocal imitation in infant-parent interaction during the first 6 months. *Journal of Reproductive and Infant Psychology, 18*, 173-187.

Kokkinaki, T., & Vitalaki, E. (2013). Exploring spontaneous imitation in infancy: A three generation inter-familial study. *Europe's Journal of Psychology*, *9*, 2259-2275.

Kotrschal, K., Schöberl, I., Bauer, B., Thibeaut, A. M., & Wedl, M. (2009). Dyadic relationships and operational performance of male and female owners and their male dogs. *Behavioural Processes*, *81*, 383–391.

Kreibig, S. D. (2010). Autonomic nervous system activity in emotion: A review. *Biological Psychology*, *84*, 394–421.

Kutsukake, N. (2007). Conspecific influences on vigilance behavior in wild chimpanzees. *International Journal of Primatology*, *28*, 907–918.

Lancet, Y., & Dukas, R. (2012). Socially influenced behaviour and learning in locusts. *Ethology*, *118*, 302–310.

Lazarus, J. (1978). Vigilance, flock size and domain of danger size in the White-fronted Goose. *Wildfowl*, *29*, 135–145.

Leadbeater, E. (2015). What evolves in the evolution of social learning? *Journal of Zoology*, *295*, 4–11.

Leadbeater, E., & Chittka, L. (2007). The dynamics of social learning in an insect model, the bumblebee (*Bombus terrestris*). *Behavioral Ecology and Sociobiology*, *61*, 1789–1796.

Leavens, D. A., Aureli, F., & Hopkins, W. D. (2001). Effects of cognitive challenge on self-directed behaviors by chimpanzees (*Pan troglodytes*). *American Journal of Primatology*, *55*, 1–14.

Leavens, D., Aureli, F., & Hopkins, W. (2004). Behavioral evidence for the cutaneous expression of emotion in a chimpanzee (*Pan troglodytes*). *Behaviour*, *141*, 979–997.

Leca, J. B., Gunst, N., & Huffman, M. A. (2010). Indirect social influence in the maintenance of the stone-handling tradition in Japanese macaques, *Macaca fuscata*. *Animal Behaviour*, *79*, 117–126.

Ledoux, J. E. (2000). Emotion circuits in the brain. *Annual Review of Neuroscience*, *23*, 155–184.

Leonardi, R., Buchanan-Smith, H. M., Dufour, V., MacDonald, C., & Whiten, A. (2010). Living together: Behavior and welfare in single and mixed species groups of capuchin (*Cebus apella*) and squirrel monkeys (*Saimiri sciureus*). *American Journal of Primatology*, *72*, 33–47.

Levine, J. M., & Zentall, T. R. (1974). Effect of a conspecific's presence on deprived rats' performance: Social facilitation vs distraction/imitation. *Animal Learning and Behavior*, *2*, 119–122.

Levy, D. A., & Nail, P. R. (1993). Contagion: A theoretical and empirical review and reconceptualization. *Genetic, Social and General Psychological Monographs*, *119*, 233–284.

Liepelt, R., Cramon, D. Y. Von, & Brass, M. (2008). What is matched in direct matching? Intention attribution modulates motor priming. *Journal of Experimental Psychology: Human Perception and Performance*, *34*, 578–591.

Lloyd, D. M., Hall, E., Hall, S., & McGlone, F. P. (2013). Can itch-related visual stimuli alone provoke a scratch response in healthy individuals? *The British Journal of Dermatology*, *168*, 106–11.

Lodder, P., Rotteveel, M., Elk, M. Van, Alejandro, E., Paolo, D., Alejandro, E., & Paolo, D. (2014). Enactivism and neonatal imitation : Conceptual and empirical considerations and clarifications, *Frontiers in Psychology*, *5*, 967.

Loewenstein, M., Ludin, a, & Schuh, M. (2006). Comparison of scratching behaviour of growing pigs with sarcoptic mange before and after treatment, employing two distinct approaches. *Veterinary Parasitology*, *140*, 334–43.

Longo, M. R., Kosobud, A., & Bertenthal, B. I. (2008). Automatic imitation of biomechanically possible and impossible actions: Effects of priming movements versus goals. *Journal of Experimental Psychology: Human Perception and Performance*, *34*, 489–501.

Lutz, C. K., Tiefenbacher, S., Jorgensen, M. J., Meyer, J. S., & Novak, M. A. (2000). Techniques for collecting saliva from awake, unrestrained, adult monkeys for cortisol assay. *American Journal of Primatology*, *52*, 93–9.

MacDonald, C., & Whiten, A. (2011). The "Living Links to Human Evolution" Research Centre in Edinburgh Zoo: A new endeavour in collaboration. *International Zoo Yearbook*, *45*, 7–17.

Macphail, E. M. (1982). *Brain and Intelligence in Vertebrates*. New York: Oxford University Press.

Macphail, E. M. (1996). Cognitive function in mammals: The evolutionary perspective. *Brain Research: Cognitive Brain Research*, *3*, 279–290.

Maestripieri, D. (1993). Maternal anxiety in rhesus macaques (*Macaca mulatta*): Measurement of anxiety and identification of anxiety eliciting situations. *Ethology*, *95*, 19–31.

Maestripieri, D., Shino, G., Aureli, F., & Troisi, A. (1992). A modest proposal : Displacement activities as an indicator of emotions in primates. *Animal Behaviour*, *44*, 967–979.

Mancini, G., Ferrari, P. F., & Palagi, E. (2013). In play we trust. Rapid facial mimicry predicts the duration of playful interactions in geladas. *PLoS ONE*, *8*, 2–6.

Martin, G. B., & Clark, R. D. (1982). Distress crying in neonates: Species and peer specificity. *Developmental Psychology*, *18*, 3–9.

Martin, P., & Bateson, P. (2007). *Measuring Behaviour*. Cambridge: Cambridge University Press.

Massen, J. J. M., Dusch, K., Eldakar, O. T., & Gallup, A. C. (2014). A thermal window for yawning in humans: Yawning as a brain cooling mechanism. *Physiology & Behavior*, *130*, 145–148.

Matthews, L. J., Paukner, A., & Suomi, S. J. (2010). Can traditions emerge from the interaction of stimulus enhancement and reinforcement learning? An experimental model. *American Anthropologist, 112*, 257–269.

McConnell, J. V. (1966). Comparative physiology: Learning in invertebrates. *Annual Review of Physiology, 28*, 107–136.

McGuigan, N., & Whiten, A. (2009). Emulation and "overemulation" in the social learning of causally opaque versus causally transparent tool use by 23- and 30-month-olds. *Journal of Experimental Child Psychology, 104*, 367–381.

McGuigan, N., Whiten, A., Flynn, E., & Horner, V. (2007). Imitation of causally opaque versus causally transparent tool use by 3- and 5-year-old children. *Cognitive Development, 22*, 353–364.

Meltzoff, A., & Moore, M. (1997). Explaining facial imitation: A theoretical model. *Early Development and Parenting, 6*, 179–192.

Meltzoff, A. N. (1988). Infant imitation after a 1-week delay: Long-term memory for novel acts and multiple stimuli. *Developmental Psychology, 24*, 470–476.

Meltzoff, A. N. (1996). The human infant as imitative generalist: A 20-year progress report on infant imitation with implications for comparative psychology. In C. M. Heyes & B. G. Galef (Eds.), *Social Learning in Animals: The Roots of Culture* (pp. 347–370). San Diego, CA: Academic Press.

Meltzoff, A. N. (2005). Imitation and other minds: The "like me" hypothesis. In S. Hurley & N. Chater (Eds.), *Perspectives on imitation: From cognitive neuroscience to social science* (Vol. 2, pp. 55–77). Cambridge, MA: MIT Press.

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

Meltzoff, A. N., & Moore, M. K. (1983). Newborn infants imitate adult facial gestures. *Child Development*, *54*, 702–709.

Mersmann, D., Tomasello, M., Call, J., Kaminski, J., & Taborsky, M. (2011). Simple mechanisms can explain social learning in domestic dogs (*Canis familiaris*). *Ethology*, *117*, 675–690.

Mettang, T. (2010). Chronic kidney disease-associated prurituc. In L. Misery & S. Ständer (Eds.), *Pruritus* (pp. 167–175). London: Springer London.

Meunier, H., Petit, O., & Deneubourg, J.-L. (2007). Social facilitation of fur rubbing in white faced capuchins. *American Journal of Primatology*, *1222*, 1210–1222.

Michel, J.-B., Shen, Y. K., Aiden, A. P., Veres, A., Gray, M. K., Pickett, J. P., … Aiden, E. L. (2011). Quantitative analysis of culture using millions of digitized books. *Science*, *331*, 176–82.

Millen, A., & Anderson, J. R. (2011). Neither infants nor toddlers catch yawns from their mothers. *Biology Letters*, *7*, 440–2.

Miller, R., Schiestl, M., Whiten, A., Schwab, C., & Bugnyar, T. (2014). Tolerance and social facilitation in the foraging behaviour of free-ranging crows (*Corvus corone corone*; *C. c. cornix*). *Ethology*, *120*, 1248–1255.

Mishra, S., & Hoon, M. (2013). The cells and circuitry for itch responses in mice. *Science*, *340*, 968–971.

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.

Mochizuki, H., Sadato, N., Saito, D. N., Toyoda, H., Tashiro, M., Okamura, N., & Yanai, K. (2007). Neural correlates of perceptual difference between itching and pain: a human fMRI study. *NeuroImage, 36*, 706–717.

Mohiyeddini, C., Bauer, S., & Semple, S. (2013). Displacement behaviour is associated with reduced stress levels among men but not women, *PLoS One, 8*, e56355.

Mohiyeddini, C., & Semple, S. (2013). Displacement behaviour regulates the experience of stress in men, *Stress, 16*, 163–171.

Monfardini, E., Redoute, J., Hadj-Bouziane, F., Hynaux, C., Fradin, J., Huguet, P., … Meunier, M. (2015). Others' sheer presence boosts brain activity in the attention (but not the motivation) network. *Cerebral Cortex*, 1–13.

Mooring, M. S., McKenzie, A. A., & Hart, B. L. (1996). Grooming in impala : Role of oral grooming in removal of ticks and effects of ticks in increasing grooming rate. *Physiology and Behavior*, *59*, 965–971.

Morris, D. (1956). The feather postures of birds and the problem of the origin of social signals. *Behaviour*, *9*, 75–113.

Morton, F. B., Brosnan, S. F., Pretot, L., Buchanan-Smith, H. M., O' Sullivan, E. P., Stocker, M., & Wilson, V. (under review). Questioning the ecological validity of using photographs to stduy social cognition in animals: An example in capuchin monkeys (*Sapajus sp.*). 1–32.

Morton, F. B., Lee, P. C., & Buchanan-Smith, H. M. (2013). Taking personality selection bias seriously in animal cognition research: A case study in capuchin monkeys (*Sapajus apella*). *Animal Cognition*, *16*, 677–84.

Mui, R., Haselgrove, M., Pearce, J., & Heyes, C. (2008). Automatic imitation in budgerigars. *Proceedings of the Royal Society of London: B*, *275*, 2547–53.

Mukamel, R., Ekstrom, A. D., Kaplan, J., Iacoboni, M., & Fried, I. (2010). Single-neuron responses in humans during execution and observation of actions. *Current Biology*, *20*, 750–756.

Murray, M. D. (1987). Effects of host grooming on louse populations. *Parasitology Today*, *3*, 276–278.

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

Nagy, E., Compagne, H., Orvos, H., Pal, A., Molnar, P., Janszky, I., … Bardos, G. (2005). Index finger movement imitation by human neonates: Motivation, learning, and left-hand preference. *Pediatric Research*, *58*, 749–753.

Nagy, E., Pilling, K., Orvos, H., & Molnar, P. (2013). Imitation of tongue protrusion in human neonates: Specificity of the response in a large sample. *Developmental Psychology*, *49*, 1628–38.

Nakayama, K. (2004). Observing conspecifics scratching induces a contagion of scratching in Japanese monkeys (*Macaca fuscata*). *Journal of Comparative Psychology*, *118*, 20–24.

Namer, B., Carr, R., Johanek, L. M., Schmelz, M., Handwerker, H. O., & Ringkamp, M. (2008). Separate peripheral pathways for pruritus in man. *Journal of Neurophysiology*, *100*, 2062–9.

Nehaniv, C. L., & Dautenhahn, K. (2002). The correspondence problem. In C. L. Nehaniv & K. Dautenhahn (Eds.), *Imitation in animals and artifacts* (pp. 41–61). Cambridge, MA: MIT Press.

Nielsen, M., & Dissanayake, C. (2004). Pretend play, mirror self-recognition and imitation: a longitudinal investigation through the second year. *Infant Behavior and Development*, *27*, 342–365.

Niemeier, V., Kupfer, J., & Gieler, U. (2000). Observations during an itch-inducing lecture. *Dermatology Psychosomatics*, *1*, 15–18.

Norscia, I., & Palagi, E. (2011). Yawn contagion and empathy in *homo sapiens*. *PLoS One*, *6*, e28472.

O'Hara, S. J., & Reeve, A. V. (2011). A test of the yawning contagion and emotional connectedness hypothesis in dogs, *Canis familiaris*. *Animal Behaviour*, *81*, 335–340.

Oaklander, A., Cohen, S., & Raju, S. (2002). Intractable postherpetic itch and cutaneous deafferentation after facial shingles. *Pain*, *96*, 9–12.

Oostenbroek, J., Slaughter, V., Nielsen, M., & Suddendorf, T. (2013). Why the confusion around neonatal imitation? A review. *Journal of Reproductive and Infant Psychology*, *31*, 328-341.

Osvath, M., & Sima, M. (2014). Sub-adult ravens synchronize their play: A case of emotional contagion? *Animal Behavior and Cognition*, *2*, 197.

O'Sullivan, E. P. (2011). Steps toward identifying automatic imitation in capuchin monkeys (*Cebus apella*): Piloting a new comparative methodology. (Unpublished masters thesis). University of Stirling, Scotland.

Ottoni, E. B., De Resende, B. D., & Izar, P. (2005). Watching the best nutcrackers: What capuchin monkeys (*Cebus apella*) know about others' tool-using skills. *Animal Cognition*, *8*, 215–219.

Palagi, E., Leone, A., Mancini, G., & Ferrari, P. F. (2009). Contagious yawning in gelada baboons as a possible expression of empathy. *Proceedings of the National Academy of Sciences of the United States of America*, *106*, 19262–19267.

Palestis, B., & Burger, J. (1998). Evidence for social facilitation of preening in the common tern. *Animal Behaviour*, *56*, 1107–1111.

Palme, B., & Möstl, E. (1997). Measurement of cortisol metabolites in faeces of

   sheep as a parameter of cortisol concentration in blood. *International Journal*

   of Mammalian Biology, *62*, 192–197.

Papoiu, a D. P., Wang, H., Coghill, R. C., Chan, Y. H., & Yosipovitch, G. (2011).

   Contagious itch in humans: a study of visual "transmission" of itch in

   atopic dermatitis and healthy subjects. *The British Journal of Dermatology*,

   164, 1299–1303.

Papousek, M., & Papouskek, H. (1989). Forms and functions of vocal matching

   in interactions between mothers and their precanonical infants. *First*

   Language, *9*, 137–157.

Parr, L. A. (2001). Cognitive and physiological markers of emotional awareness

   in chimpanzees (*Pan troglodytes*). *Animal Cognition*, *4*, 223–229.

Patel, K. N., & Dong, X. (2010). An itch to be scratched. *Neuron*, *68*, 334–9.

Paulus, M. (2014). How and why do infants imitate? An ideomotor approach to

   social and imitative learning in infancy (and beyond). *Psychonomic bulletin*

   & review, *8*(2), 77–81.

Paukner, A., & Anderson, J. R. (2006). Video-induced yawning in stumptail

   macaques (*Macaca arctoides*). *Biology Letters*, *2*, 36–8.

Paukner, A., Suomi, S. J., Visalberghi, E., & Ferrari, P. F. (2009). Capuchin monkeys display affiliation towards humans who imitate them. *Science*, *325*, 880–883.

Paulus, M., Hunnius, S., Van Elk, M., & Bekkering, H. (2012). How learning to shake a rattle affects 8-month-old infants' perception of the rattle's sound: Electrophysiological evidence for action-effect binding in infancy. *Developmental Cognitive Neuroscience*, *2*, 90–96.

Pavani, S., Maestripieri, D., Schino, G., Turilazzi, P. G., & Scucchi, S. (1991). Factors influencing scratching behaviour in long-tailed macaques (*Macaca fascicularis*). *Folia Primatologica*, *57*, 34–38.

Pawlby, S. (1977). Imitative interaction. In H. Schaffer (Ed.), *Studies in mother-infant interaction* (pp. 203–233). London: Academic Press.

Pays, O., Goulard, M., Blomberg, S. P., Goldizen, A. W., Sirot, E., & Jarman, P. J. (2009). The effect of social facilitation on vigilance in the eastern gray kangaroo, *Macropus giganteus*. *Behavioral Ecology*, *20*, 469–477.

Pérez-Cembranos, A., & Pérez-Mellado, V. (2014). Local enhancement and social foraging in a non-social insular lizard. *Animal Cognition*, *18*, 629–637.

Perry, S. (2011). Social traditions and social learning in capuchin monkeys (*Cebus*). *Philosophical Transactions of the Royal Society of London: B*, *366*, 988–996.

Petit, O., Gautrais, J., Leca, J. B., Theraulaz, G., & Deneubourg, J.L. (2009). Collective decision-making in white-faced capuchin monkeys. *Proceedings of the Royal Society of London: B,276*, 3495–3503.

Piaget, J. (1962). *Play, dreams and imitation in childhood*. New York: Norton. (Translated from French. First English edition published, 1951)

Platek, S. M., Critton, S. R., Myers, T. E., & Gallup, G. G. (2003). Contagious yawning: the role of self-awareness and mental state attribution. *Brain Research. Cognitive Brain Research*, *17*, 223–227.

Plotnik, J. M., & de Waal, F. B. M. (2014). Asian elephants (*Elephas maximus*) reassure others in distress. *PeerJ, 2*, e278.

Plowman, A. B., Jordan, N. R., Anderson, N., Condon, E., & Fraser, O. (2005). Welfare implications of captive primate population management: behavioural and psycho-social effects of female-based contraception, oestrus and male removal in hamadryas baboons (*Papio hamadryas*). *Applied Animal Behaviour Science*, *90*, 155–165.

Polizzi di Sorrentino, E., Schino, G., Tiddi, B., & Aureli, F. (2012). Scratching as a window into the emotional responses of wild tufted capuchin monkeys. *Ethology*, *118*, 1072–1084.

Pomerantz, O., & Terkel, J. (2009). Effects of positive reinforcement training techniques on the psychological welfare of zoo-housed chimpanzees (*Pan troglodytes*). *American Journal of Primatology*, *71*, 687–695.

Press, C., Gillmeister, H., & Heyes, C. (2007). Sensorimotor experience enhances automatic imitation of robotic action. *Proceedings of the Royal Society of London: B.*, *274*, 2509–2514.

Preston, S. D., & de Waal, F. B. M. (2002). Empathy: Its ultimate and proximate bases. *The Behavioral and Brain Sciences*, *25*, 1-71.

Price, E., & Caldwell, C. A. (2007). Artificially generated cultural variation between two groups of captive monkeys, *Colobus guereza kikuyuensis*. *Behavioural Processes*, *74*, 13–20.

Prinz, W. (1997). Perception and action planning. *European Journal of Cognitive Psychology*, 9, 129–154.

Prinz, W. (2005). An ideomotor approach to imitation. In S. Hurley, & N. Chater (Eds.), *Mechanisms of imitation and imitation in animals* (pp. 141-156). Cambridge, MA: MIT Press.

Provine, R. R. (1992). Contagious yawning and laughter: Significance for sensory feature detection, motor pattern generation, imitation, and the evolution of social behavior. In C. M. Heyes & B. G. Galef (Eds.), *Social Learning in Animals: The Roots of Culture* (pp. 179-208). San Diego, CA: Academic Press.

Raber, H. (1948). Analyse des Balzverhaltens eines domestizierten Truthahns (*Meleagris*). *Behaviour*, *1*, 237–266.

Range, F., & Huber, L. (2007). Attention in common marmosets: Implications for social-learning experiments. *Animal Behaviour*, *73*, 1033–1041.

Range, F., Huber, L., & Heyes, C. (2011). Automatic imitation in dogs. *Proceedings of the Royal Society of London: B,278*, 211–217.

Rawlins, J., Arbib, M. A., Blackmore, S., Jones, S. S., Kinsbourne, M., Donald, M., & Whiten, A. (2005). Commentary and discussion on mechanisms of imitation. In S. Hurley & N. Chater (Eds.), *Perspectives on imitation: From cognitive neuroscience to social science*.Cambridge, MA: MIT Press.

Ray, E., & Heyes, C. (2011). Imitation in infancy: The wealth of the stimulus. *Developmental Science*, *14*, 92–105.

Repacholi, B. M., & Gopnik, A. (1997). Early reasoning about desires: Evidence from 14- and 18-month-olds. *Developmental Psychology*, *33*, 12–21.

Rescorla, R. A. (1988). Pavlovian conditioning: It's not what you think it is. *American Psychologist, 43*, 151–160.

Reynaud, A. J., Guedj, C., Hadj-Bouziane, F., Meunier, M., & Monfardini, E. (2015). Social facilitation of cognition in rhesus monkeys: Audience vs. coaction. *Frontiers in Behavioral Neuroscience, 9*, 1–5.

Reynolds, C. W. (1987). Flocks, herds and schools: A distributed behavioral model. *Computer Graphics, 21*, 25–34.

Richner, H. (1989). Habitat-specific growth and fitness in carrion crows (*Corvus corone corone*). *The Journal of Animal Ecology, 58*, 427-440.

Rimpley, K., & Buchanan-Smith, H. M. (2013). Reliably signalling a startling husbandry event improves welfare of zoo-housed capuchins (*Sapajus apella*). *Applied Animal Behaviour Science, 147*, 205–213.

Rizzolatti, G., & Arbib, M. A. (1998). Language within our grasp. *Trends in Neurosciences, 21*, 188–194.

Rizzolatti, G., & Craighero, L. (2004). The mirror-neuron system. *Annual Review of Neuroscience, 27*, 169–192.

Rizzolatti, G., Fadiga, L., Gallese, V., & Fogassi, L. (1996). Premotor cortex and the recognition of motor actions. *Cognitive Brain Research, 3*, 131–41.

Rizzolatti, G., & Fogassi, L. (2001). Neurophysiological mechanisms underlying the understanding and imitation of action. *Nature Reviews, 2*, 661-670.

Rizzolatti, G., & Fogassi, L. (2014). The mirror mechanism: Recent findings and perspectives. *Philosophical Transactions of the Royal Society of London: B,369*, 20130420.

Roberts, G. (1996). Why individual vigilance declines as group size increases. *Animal Behaviour, 51*, 1077–1086.

Robinette, R. L., & Ha, J. C. (2001). Social and ecological factors influencing vigilance by northwestern crows, *Corvus caurinus*. *Animal Behaviour, 62*, 447–452.

Roelofs, K., Hagenaars, M. a, & Stins, J. (2010). Facing freeze: Social threat induces bodily freeze in humans. *Psychological Science, 21*, 1575–1581.

Rosenbaum, M., & Ayllon, T. (1981). The behavioral treatment of neurodermatitis through habit-reversal. *Behaviour Research and Therapy, 19*, 313–318.

Rosenthal, S. B., Twomey, C. R., Hartnett, A. T., Wu, H. S., & Couzin, I. D. (2015). Revealing the hidden networks of interaction in mobile animal groups allows prediction of complex behavioral contagion. *Proceedings of the National Academy of Sciences, 112*, 201420068.

Rothman, S. (1941). Physiology of itching. *Physiological Reviews*, *21*, 357–381.

RStudio Core Team. (2014). *RStudio: Integrated development environment for R (Version ″.1) [Computer software]*. Bostan, MA.

Russon, A. E., & Galdikas, B. M. (1993). Imitation in free-ranging rehabilitant orangutans (*Pongo pygmaeus*). *Journal of Comparative Psychology*, *107*, 147–161.

Sarin, S., & Dukas, R. (2009). Social learning about egg-laying substrates in fruitflies. *Proceedings of the Royal Society of London: B, 276*, 4323–4328.

Schino, G., Maestripieri, D., Scucchi, S., & Turillazzi, P. (1990). Social tension in familiar and unfamiliar pairs of long-tailed macaques. *Behaviour*, *113*, 264–272.

Schino, G., Perretta, G., Taglioni, A., Monaco, V., & Troisi, A. (1996). Primate displacement activities as an ethopharmacological model of anxiety. *Anxiety*, *2*, 186–191.

Schmidt, A., Aurich, J., Möstl, E., Müller, J., & Aurich, C. (2010). Changes in cortisol release and heart rate and heart rate variability during the initial training of 3-year-old sport horses. *Hormones and Behavior*, *58*, 628–636.

Schneider, E., Rolli-Derkinderen, M., Arock, M., & Dy, M. (2002). Trends in histamine research: new functions during immune responses and hematopoiesis. *Trends in Immunology*, *23*, 255–263.

Schuster, S., Wöhl, S., Griebsch, M., & Klostermeier, I. (2006). Animal cognition: how archer fish learn to down rapidly moving targets. *Current Biology*, *16*, 378–383.

Sclafani, V., Norscia, I., Antonacci, D., & Palagi, E. (2012). Scratching around mating: factors affecting anxiety in wild Lemur catta. *Primates*, *53*, 247–54.

Sevenster, P. (1961). A causal analysis of a displacement activity (fanning in *Gasterosteus aculeatur l.*). *Behaviour*, Supplement(9), 1–170.

Shaffer, J. P. (1986). Modified sequentially rejective multiple test procedures. *Journal of the American Statistical Association*, *81*, 826–831.

Shettleworth, S. J. (1998). *Cognition, Evolution, and Behaviour*. New York: Oxford University Press.

Shettleworth, S. J. (2010). Clever animals and killjoy explanations in comparative psychology. *Trends in Cognitive Sciences*, *14*, 477–481.

Silva, K., Bessa, J., & de Sousa, L. (2012). Auditory contagious yawning in domestic dogs (*Canis familiaris*): first evidence for social modulation. *Animal Cognition*, *15*, 721–724.

Simpson, A., & Riggs, K. J. (2011). Under what conditions do children have difficulty in inhibiting imitation? Evidence for the importance of planning specific responses. *Journal of Experimental Child Psychology*, *109*, 512–524.

Simpson, A., Riggs, K. J., Beck, S. R., Gorniak, S. L., Wu, Y., Abbott, D., & Diamond, A. (2012). Refining the understanding of inhibitory processes: how response prepotency is created and overcome. *Developmental Science*, *15*, 62–73.

Simpson, E. A, Murray, L., Paukner, A., & Ferrari, P. F. (2014). The mirror neuron system as revealed through neonatal imitation : Presence from birth , predictive power and evidence of plasticity. *Philosophical Transactions of the Royal Society of London: B,369*, 20130289.

Simpson, S. J., Raubenheimer, D., Charleston, M. A., & Clissold, F. J. (2010). Modelling nutritional interactions: from individuals to communities. *Trends in Ecology and Evolution*, 25, 53–60.

Stel, M., Van Baaren, R. B., & Vonk, R. (2008). Effects of mimicking : Acting prosocially by being emotionally moved. *European Journal of Social Psychology*, *38*, 965–976.

Strandburg-Peshkin, A., Farine, D. R., Couzin, I. D., & Crofoot, M. C. (2015). Shared decision-making drives collective movement in wild baboons. *Science*, *348*, 1358–1361.

Stürmer, B., Aschersleben, G., & Prinz, W. (2000). Correspondence effects with manual gestures and postures: a study of imitation. *Journal of Experimental Psychology: Human Perception and Performance*, *26*, 1746–1759.

Sueur, C., Deneubourg, J. L., & Petit, O. (2012). From social network (centralized vs. decentralized) to collective decision-making (unshared vs. shared consensus). *PLoS One, 7*.

Tennie, C., Call, J., & Tomasello, M. (2006). Push or pull: Imitation vs. emulation in great apes and human children. *Ethology*, *112*, 1159–1169.

Tinbergen, N., & Iersel, J. Van. (1947). Displacement reactions in the three-spined stickleback. *Behaviour*, *1*, 56–63.

Tolman, C. W. (1964). Social facilitation of feeding behaviour in the domestic chick. *Animal Behaviour*, *12*, 245–251.

Tomasello, M. (1998). Do apes ape? In C. M. Heyes & B. G. Galef (Eds.), *Social Learning in Animals: The Roots of Culture* (pp. 319-346). San Diego, CA: Academic Press.

Tomasello, M., & Call, J. (1997). *Primate Cognition*. New York: Oxford University

Press.

Tomasello, M., Carpenter, M., Call, J., Behne, T., & Moll, H. (2005).

Understanding and sharing intentions: The origins of cultural cognition,

Behavioral and Brain Science, *28*, 675–735.

Tomasello, M., Davis-Dasilva, M., Camak, L., & Bard, K. (1987). Observational

learning of tool-use by young chimpanzees. *Human Evolution*, *2,* 175–183.

Topál, J., Byrne, R. W., Miklósi, A., & Csányi, V. (2006). Reproducing human

actions and action sequences: "Do as I Do!" in a dog. *Animal Cognition*, *9*,

355–67.

Travis, L. E. (1925). The effect of a small audience upon eye-hand coordination.

The Journal of Abnormal and Social Psychology, *20*, 142–146.

Treves, A. (1998). The Influence of group size and neighbors on vigilance in two

species of arboreal monkeys. *Behaviour*, *135*, 453–481.

Treves, A. (1999). Within-group vigilance in red colobus and redtail monkeys.

American Journal of Primatology, *48*, 113–126.

Troisi, A. (2002). Displacement activities as a behavioral measure of stress in

nonhuman primates and human subjects. *Stress*, *5*, 47–54.

Troisi, A., & Schino, G. (1987). Environmental and social influences on autogrooming behaviour in a captive group of Java monkeys. *Behaviour*, *100*, 292-302.

Troisi, A., Schino, G., D' Antoni, M., Pandolfi, N., Aureli, F., & D, Amato, F. R. (1991). Scratching as a behavioural index of anxiety in macaque mothers. *Behavioral and Neural Biology*, *56*, 307–313.

Tse, W. S., & Bond, A. J. (2004). Relationship between baseline cortisol, social functioning and depression: a mediation analysis. *Psychiatry Research*, *126*, 197–201.

Umiltà, M., Escola, L., Intskirveli, I., Grammont, F., Rochat, M., Caruana, F., … Rizzolatti, G. (2008). When pliers become fingers in the monkey motor system. *Proceedings of the National Academy of Sciences of the United States of America*, *105*, 2209–13.

Umiltà, M., Kohler, E., Gallese, V., Fogassi, L., Fadiga, L., Keysers, C., & Rizzolatti, G. (2001). I know what you are doing: A neurophysiological study. *Neuron*, *31*, 155–65.

Vale, G. L., Flynn, E. G., & Kendal, R. L. (2012). Cumulative culture and future thinking: Is mental time travel a prerequisite to cumulative cultural evolution? *Learning and Motivation*, *43*, 220–230.

van Baaren, R. B., Janssen, L., Chartrand, T. L., & Dijksterhuis, A. (2009). Where is the love? The social aspects of mimicry. *Philosophical Transactions of the Royal Society of London: B,364*, 2381–2389.

van Bergen, Y., Coolen, I., & Laland, K. N. (2004). Nine-spined sticklebacks exploit the most reliable source when public and private information conflict. *Proceedings of the Royal Society of London: B,271*, 957–962.

van de Waal, E., & Bshary, R. (2011). Social-learning abilities of wild vervet monkeys in a two-step task artificial fruit experiment. *Animal Behaviour, 81*, 433–438.

van de Waal, E., Claidière, N., & Whiten, A. (2013). Social learning and spread of alternative means of opening an artificial fruit in four groups of vervet monkeys. *Animal Behaviour, 85*, 71–76.

van de Waal, E., & Whiten, A. (2012). Spontaneous emergence, imitation and spread of alternative foraging techniques among groups of vervet monkeys. *PLoS One, 7*, e47008.

Vanderwert, R. E., Simpson, E. A., Paukner, A., Suomi, S. J., Fox, N. a., & Ferrari, P. F. (2015). Early social experience affects neural activity to affiliative facial gestures in newborn nonhuman primates. *Developmental Neuroscience, 37*, 243-252.

Vasconcelos, M., Hollis, K., Nowbahari, E., & Kacelnik, A. (2012). Pro-sociality without empathy. *Biology Letters*, *8*, 910–912.

Vick, S.-J., Bovet, D., & Anderson, J. R. (2010). How do African grey parrots (*Psittacus erithacus*) perform on a delay of gratification task? *Animal Cognition*, *13*, 351–8.

Videan, E. N., Fritz, J., Schwandt, M., & Howell, S. (2005). Neighbor effect: Evidence of affiliative and agonistic social contagion in captive chimpanzees (*Pan troglodytes*). *American Journal of Primatology*, *66*, 131–44.

Vining, R. F., McGinley, R. A., Maksvytis, J. J., & Ho, K. Y. (1983). Salivary cortisol: A better measure of adrenal cortical function than serum cortisol. *Annals of Clinical Biochemistry*, *20*, 329–335.

Visalberghi, E. (1993). Capuchin monkeys: a window into tool use in apes and humans. In K. Gibson & T. Ingold (Eds.), *Tools, language and cognition in human evolution.* (pp. 138–150). Cambridge: Cambridge University Press.

Visalberghi, E., & Addessi, E. (2001). Social facilitation of eating novel food in tufted capuchin monkeys (*Cebus apella*): input provided by group members and responses affected in the observer. *Animal Cognition*, *4*, 297–303.

Visalberghi, E., & Fragaszy, D. M. (2001). " Do monkeys ape ?"— Ten years after. In E. Dupoux (Ed.), *Language, Brain, and Cognitive Development* (pp. 472–499). Cambridge, MA: MIT Press.

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

Voelkl, B., & Huber, L. (2007a). Common marmosets (*Callithrix jacchus*) do not utilize social information in three simultaneous social foraging tasks. *Animal Cognition*, *10*, 149–158.

Voelkl, B., & Huber, L. (2007b). Imitation as faithful copying of a novel technique in marmoset monkeys. *PLoS One*, *2*, e611.

von Rohr, C. R., van Schaik, C. P., Kissling, A., & Burkart, J. M. (2015). Chimpanzees' bystander reactions to infanticide: An evolutionary precursor of social norms? *Human nature, 26*, 143–60.

Waters, S. F., West, T. V, & Mendes, W. B. (2014). Stress contagion: Physiological covariation between mothers and infants. *Psychological Science, 25*, 934-942.

Watson, C. F. I., Buchanan-Smith, H. M., & Caldwell, C. A. (2014). Call playback artificially generates a temporary cultural style of high affiliation in marmosets. *Animal Behaviour, 93*, 163-171.

Watson, C. F. I., & Caldwell, C. A. (2010). Neighbor effects in marmosets: social contagion of agonism and affiliation in captive *Callithrix jacchus*. *American Journal of Primatology*, *72*, 549–558.

Waxer, P. H. (1977). Nonverbal cues for anxiety: An examination of emotional leakage, *Journal of Abnormal Psyhology*, *86*, 306–314.

Webster, M. M., & Laland, K. N. (2012). The learning mechanism underlying public information use in ninespine sticklebacks (*Pungitius pungitius*). *Journal of Comparative Psychology*, *127*, 154–165.

Webster, M. M., & Laland, K. N. (2013). Local enhancement via eavesdropping on courtship displays in male guppies, *Poecilia reticulata*. *Animal Behaviour*, *86*, 75–83.

Whiten, A. (1998). Imitation of the sequential structure of actions by chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, *112*, 270–281.

Whiten, A. (2000). Primate culture and social learning. *Cognitive Science*, *24*, 477–508.

Whiten, A., Goodall, J., McGrew, W. C., Nishida, T., Reynolds, V., Sugiyama, Y., … Boesch, C. (1999). Cultures in chimpanzees. *Nature, 399,* 682–685.

Whiten, A., & Ham, R. (1992). On the nature and evolution of imitation in the animal kingdom: reappraisal of a century of research. *Advances in the Study of Behavior*, *21*, 239–283.

Whiten, A., Horner, V., Litchfield, C. A., & Marshall-Pescini, S. (2004). How do apes ape? *Learning & Behavior*, *32*, 36–52.

Whiten, A., Horner, V., & Marshall-pescini, S. (2005). Selective imitation in child and chimpanzee: A window on the construal of others' actions. In S. Hurley & N. Chater (Eds.), *Perspectives on imitation: From cognitive neuroscience to social science* (Vol. 1, pp. 263–283). Cambridge, MA: MIT Press.

Whiten, A., McGuigan, N., Marshall-Pescini, S., & Hopper, L. M. (2009). Emulation, imitation, over-imitation and the scope of culture for child and chimpanzee. *Philosophical Transactions of the Royal Society of London: B,364*, 2417–2428.

Whiten, A., & van Schaik, C. P. (2007). The evolution of animal "cultures" and social intelligence. *Philosophical Transactions of the Royal Society of London: B,362*, 603–20.

Wicker, B., Keysers, C., Plailly, J., Royet, J. P., Gallese, V., & Rizzolatti, G. (2003). Both of us disgusted in my insula: The common neural basis of seeing and feeling disgust. *Neuron, 40*, 655–64.

Wickham, H. (2009). *ggplot2: elegant graphics for data analysis*. New York: Springer.

Wilkinson, A., Kuenstner, K., Mueller, J., & Huber, L. (2010). Social learning in a non-social reptile (*Geochelone carbonaria*). *Biology Letters*, *6*, 614–616.

Wolters, S., & Zuberbühler, K. (2013). Mixed-species associations of diana and campbell 's monkeys : The costs and benefits of a forest phenomenon. *Behaviour*, *140*, 371–385.

Yamamoto, Y., Yamazaki, S., Hayashino, Y., Takahashi, O., Tokudo, Y., Shimbo, T., … Fukuhara, S. (2009). Association between frequency of pruritic symptoms and perceived psychological stress. *Archives of Dermatology*, *145*, 1384–1388.

Yosipovitch, G., Fast, K., & Bernhard, J. D. (2005). Noxious heat and scratching decrease histamine-induced itch and skin blood flow. *The Journal of Investigative Dermatology*, *125*, 1268–1272.

Zahn-Waxler, C., & Radke-Yarrow, M. (1990). The origins of empathic concern. *Motivation and Emotion*, *14*, 107–130.

Zajonc, R. (1965). Social Facilitation. *Science*, *149*, 269–274.

Zajonc, R. B., & Sales, S. M. (1966). Social facilitation of dominant and subordinate responses. *Journal of Experimental Social Psychology*, *2*, 160–168.

Zeigler, H. (1964). Displacement activity and motivational theory: A case study in the history of ethology. *Psychological Bulletin*, *61*, 362–376.

Zentall, T. R. (2006). Imitation: definitions, evidence, and mechanisms. *Animal Cognition*, *9*, 335–353.

Zentall, T. R. (2012). Perspectives on observational learning in animals. *Journal of Comparative Psychology*, *126*, 114–128.

Zentall, T. R., Sutton, J. E., & Sherburne, L. M. (1996). True imitative learning in pigeons. *Psychological Science*, *7*, 343–346.

Zuur, A., Ieno, E., Walker, N., Saveliev, A., & Smith, G. (2009). *Mixed effects models and extensions in ecology with R*. New York: Springer.