INTERACTIVE BEHAVIOUR IN PIGEONS: VISUAL DISPLAY INTERACTIONS AS A MODEL FOR VISUAL COMMUNICATION

by

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Abstract

Four experiments are presented that explore social interactivity in a visually communicating species: the pigeon, *Columba livia*. A closed-loop teleprompter system was used to isolate, control and manipulate social contingency in a natural courtship interaction. Experiment 1 tested different ways to measure pigeon behaviour and developed an automatic method for measuring the pigeon’s circle walking display using motion energy analysis. In Experiment 2, the subject’s courtship behaviour towards the video image of an opposite sex partner streamed live (Live), was compared with their behaviour towards a pre-recorded video image of the same partner (Playback). The only difference between the Live and Playback condition was the presence or absence of social contingency. The results showed that pigeons behaved interactively: their behaviour was determined, in part, by the social contingencies between visual signals. To investigate what types of social contingencies are behaviourally relevant, the effects of the partner’s facing direction and the timing of social contingencies on behaviour were investigated in Experiment 3 and 4, respectively. To manipulate partner facing direction, the camera was rotated so that the partner appears to be courting 90° away from the subject. To manipulate social timing, three time delays, 1, 3 and 9s, were implemented within the closed-circuit communication. In Experiment 4, the context-specificity of interactive behaviour was also investigated by testing behavioural sensitivity to social contingency and timing in both opposite sex and same sex social interactions. The results showed that the partner’s facing direction did not significantly influence behaviour, whereas the timing of social contingencies had a significant impact on behaviour: in courtship only. These findings suggest that temporal relations between display bouts in courtship are behaviourally relevant. A post hoc analysis was then used to evaluate the behavioural relevance of two social contingencies in particular: partner responsiveness and simultaneous display. The results showed that females may be sensitive to the male responsiveness in courtship. Also, simultaneous display appeared to create a perceptual interaction which acted to potentiate the courtship dynamic. These studies provide a basis for further developing the pigeon and its courtship behaviour as a model for visual communication.
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Co-Authorship

These experiments were all designed, conducted and interpreted by the author. My supervisor, Dr. Nikolaus F. Troje provided continuous input and supervision. Daniel Saunders assisted with the work presented in Experiment 1. He helped to set up the EyesWeb motion analysis software for motion energy analysis and assisted with developing the procedure for processing the motion energy data to measure the pigeon’s courtship display.
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Chapter 1
Introduction

From its early beginnings, animal vision has evolved to process the rich information contained in other animals’ body movements (Troje 2008; Nakayama 2010). Concurrently, species’ motor systems have evolved behaviors designed to incite action in other animals’ behaviour (Krebs and Dawkins 1984). In the common scientific practice of studying social perception and behaviour in isolation, it is all too easy to forget that these two processes cannot and do not exist, evolve, occur, or function independently of one another. It is not surprising then, that some of the most exciting and thought-provoking research in social neuroscience, psychology and biology today is that which captures the fundamental interplay between social perception and behaviour by investigating these processes within their natural context: social interaction.

Animal social interactions are commonly described as a chain of reciprocal signals where each is successively ‘released’ by stimuli present in the signal preceding it (Tinbergen 1952; Tinbergen 1962). A pervasive problem for the ethologist in understanding social interaction is the inability to know the ‘interactive code’ which is used: what is the meaning of a given behaviour, and how is this meaning affected by other behaviours in the chain? For the purposes of the investigations presented here, social interactivity is defined as the degree to which a social behaviour depends on other behaviours in the chain. Four levels of social interactivity can be described: non-interactive behaviour is unrelated to other behaviours, socially reactive behaviour is ‘released’ by a social stimulus but is not necessarily communicative in function (Tinbergen 1952), socially responsive behaviour functions as a communicative reply to a preceding social signal (Tinbergen 1962) and interactive behaviour may be influenced, not only by the stimuli in
the signals immediately preceding it, but by a number of previous signals as well as the relationships between them (Fong et al. 2003).

*Interactive behaviour*, which is the focus of this thesis, is essentially a behavioural sensitivity to the nature of relations between social signals. Like billiard balls hitting each other on a pool table, social actions are mutually dependent in predictable ways (Watson 1985; Gergely and Watson 1999). *Social contingency* is one way to define these relations; it refers to an above-chance probabilistic relationship between the actions of two interactants (Moran et al. 1992). The timing, spacing and relational qualities between socially contingent behaviours can also vary in informative ways. Within interactions, social contingency along with consistencies in the timing and spacing between signals, can give rise to *social coherence*, an observable agreement between the movements and behaviors of different organisms. Social coherence is used here as a broad term to encompass a wide range of phenomenon, from simple instances of synchronized activity, like bioluminescent insects flashing in unison (e.g. Greenfield 1994), to other forms of temporal or spatial consistency, such as the patterns emerging between prey animals evading a single predator (Di Paolo 2000). In human conversation for example, researcher have constructed a measure of social coherence called *interactional synchrony*: defined as the degree of coincidence between the boundaries of body movements of two people in conversation (Condon and Ogston 1994; Bernieri 1988). For researchers, knowing the ‘interactive code’ of animal interactions means knowing which social contingencies or patterns of social coherence within interactions that influence behaviour.

To date, the study of interactive behaviour in non-human animals has been largely biased towards investigating vocal interactions. Song behaviour is often very clearly interactive; vocal contingencies within the song dialogue give rise to conspicuous coherent structures (e.g. turn-taking, overlapping, and matching) that critically shape the meaning of songs and their influence on social outcomes (Hall, 2009; Naguib 2006; Malacarne, 1991; Haimoff, 1986; Todt and Naguib
Social interaction and the ‘interactive code’, however, cannot be fully elucidated by focusing on vocal elements alone. Communications are rarely strictly visual or strictly vocal, but rather, commonly depend on visual and vocal transmissions as well as on any interactions occurring between them (e.g. Williams 2001). Thus, to obtain even a very basic understanding of interactive social behaviour, investigating such processes in both the vocal and the visual channel is a fundamental step. At present, interactive behaviour in the visual channel is poorly understood and only rarely studied directly. One reason may be that the contingencies and coherence within visual communications are characteristically subtle and difficult to identify. Typically, the relations between interactants movements, gestures, postures and actions lack overt synchrony, turn-taking or other forms of ritualized structure, like that which has attracted attention to song interactions. The lack of exaggeration in the structure of visual interaction, however, does not preclude its presence and importance in determining the social outcomes of communications. Although there are special challenges to studying social interactivity in the visual domain, in order to understand social interaction, it is essential to gain an understanding of the structural patterns underlying non-verbal dialogues.

1.1 Overview of this thesis work

The primary goal of this thesis work is to investigate interactive behaviour in the visual communication channel using an animal model, the pigeon (Columba livia). The hope is to provide a preliminary description of social interactivity in the pigeon and to establish a basis for further developing the pigeon as a model of interactive behaviour in the visual domain. The ultimate goal is to facilitate future work investigating the neural substrates of social interactivity.

Unlike all other studies investigating interactive behaviour in animals to date (which will be described below), we use a controlled experimental design to examine whether pigeons behave interactively in visual communications. The challenge of testing an animal’s behavioral
sensitivity to social contingency is in staging a social interaction that maintains natural social contingency while achieving the controlled manipulation of those same social contingencies. Short of embodying a pigeon ourselves, a technique approximated by semi-natural interactive models (robotic - Patricelli et al. 2006, animated - Watanabe and Troje 2006, or video - Ord and Evans 2002), the perfect experiment is realistically impossible. The current work uses a method of testing the effects of social contingency on behaviour that achieves both a high degree of naturalness and experimental control. The double closed-loop teleprompter interface is a paradigm that was pioneered in work studying human infant-mother interactions and is an established way to conduct a controlled manipulation of social contingency (Murray and Trevarthen 1985; Bigelow et al. 1996; Hains and Muir 1996; Nadel et al. 1999; Bigelow and DeCoste 2003; Striano et al. 2006). In traditional use, a teleprompter is an electronic device that, unseen by the audience, scrolls a prepared speech as a prompting aid to a speaker on television. A double closed-loop teleprompter interface allows each subject to be filmed from a hidden camera placed behind the live video image of the other subject. This setup gives both members of the interaction the experience of being engaged in a natural, real-time (Live) social interaction with each other. A pigeons’ behaviour in this Live condition can be compared with their responses towards a previously recorded social partner (Playback). Since the Playback condition uses the footage recorded during the pair’s previous Live condition, these stimuli are identical, except for the presence or absence of social contingency. In the Playback condition the social partner cannot react or respond contingency towards the subject’s actions, but in the Live condition both animals can interact responsively and contingently towards one another’s actions. To the author’s knowledge, this is the first use of this paradigm to study social contingency sensitivity in a non-human species.

Before presenting the experiments, two introductory chapters review what is currently understood about interactive behaviour in the visual communication channel. Chapter 1 provides
an overview of interactive social behaviour and its suggested function in animal communication. 

Chapter 2 reviews the mechanisms that have been proposed to explain how social contingency can come to influence behaviour during social interaction.

In Chapter 3, four experiments are presented. The first, Experiment 1, tested the validity of an automated technique for measuring the pigeon’s courtship behaviour using motion energy analysis. In Experiment 2 we began to investigate whether pigeon courtship behaviour is interactive or not by using a simple, controlled design: by comparing the subject’s courtship response towards a partner presented Live in the teleprompter apparatus with their response towards a partner presented in Playback conditions (Murray and Trevarthen 1985). In finding evidence for interactive behaviour, the next two experiments, Experiment 3 and Experiment 4, were designed to narrow down the possible social contingencies which might form the basis of the pigeon’s sensitivity. We did this by examining to what degree interactive behaviour relies on the spacing or timing between social signals. The spatial manipulations (Experiment 3) were achieved by moving the teleprompter camera 90 ° away from its original location; the partner’s behaviour is manipulated to appear as if it is directed 90 ° away from the subject. The temporal manipulations (Experiment 4) were achieved with three time delays, 1s, 3s and 9s, chosen to approximate the duration of visual signals in the pigeon’s behavioural repertoire (the bow, the circle and the circle walking bout, respectively) and to manipulate the temporal contiguity of social contingency. In Experiment 4, the context specificity of interactive behaviour was also tested by conducting the experiment in both same sex (rivalry) and opposite sex pairs (courtship). The pattern of results led us to hypothesize about two specific types of social contingencies that might be relevant to courting pigeons. To test these ideas, we conducted a dyadic post hoc analysis of the data collected in Experiment 4.
In the concluding chapter, an attempt is made at revising the framework for explaining the mechanisms underlying interactive social behaviour and the possible neural mechanisms underlying these processes are discussed.

1.2 Revealing social interactivity in animals

Since the 1940s, scientists studying social behaviour have relied on using simple ‘social’ dummies, such as cardboard cut-outs, to vary visual features like colour, brightness, shape and size (Tinbergen 1965). While these methods have generated landmark discoveries in ethology, most of these controlled stimuli lack arguably the most critical feature of visual signals, motion. In this regard, video playback research, the use of video images in place of natural stimuli, marks a giant breakthrough for the study of visual communication (D’eath 1998). With video, ethologists can vary or hold constant the dynamic features of social signals. Evans and Marler (1991) were the first to demonstrate these methods in using video playbacks of female hens (Gallus domesticus) to show the influence of their presence on male alarm calling behaviour. Since then, video playback methods have been employed for studying visual communications in a diverse variety of animal species, including invertebrates (Aizawa 1998; Clark and Uetz 1990), fish (Rowland 1995; Trainor and Basolo 2000; Rosenthal et al. 2004; Kodric-Brown and Nicoletto 1997), reptiles (Macedonia et al. 1994; Ord and Evans 2002; Van Dyk and Evans 2008) and birds (Galoch and Bischof 2007; Frost and Troje 1998; Shimizu 1998; McQuoid and Galef 1993; Watanabe et al. 1993; Bird and Emery 2008).

In the field of video playback research, the importance of social interactivity has become a re-occurring point of discussion (e.g. Kodric-Brown and Nicoletto 1997; Patton et al. 2009). While video creates a nearly natural social stimulus, pre-recording behaviour necessarily precludes the formation of natural reciprocal responsiveness between the subject and the partner displayed on video. Any social signal under investigation is necessarily stripped of the social
reactions and responses that it likely functions to elicit. In destroying social contingencies, the structure of interaction may break down and the meaning of the signal under investigation may change.

The evidence that visual communication is interactive – that social contingencies do influence behaviour – comes from studies that observe differences in the subject’s behaviour that depend on whether that partner is displayed live (across clear glass) or on video playback. Of course, with this design, the question of whether social contingency influences behaviour is always confounded since there are a number of fairly drastic discrepancies between a video image and a live conspecific. The colour of a video display, the range of depth cues available and the flicker on the video screen are all discrepant from the quality of social partners in the real world (see D’eath 1998, Schlupp 2000, Oliveira 2000, and Fleishman 2000). It is also possible that the differences in subject behaviour towards a partner presented on video and towards a partner presented live are due, at least in part, to the sensitivity of the subject’s interactive behaviour to the variations in social contingency across the two situations.

Despite the presence of confounds, there is accumulating evidence to suggest that absence of social contingency disrupts the subject’s ability to form or act on social preferences. For instance, hens (Gallus Domesticus) generally spend more time in proximity with familiar cage mates than with strangers. However, if the same familiar and unfamiliar conspecifics are shown on video, hens suddenly show no preference for their familiar companions (D’eath and Dawkins 1996). Female zebra finches (Taeniopygia guttata) prefer their mates over other males when greeting these males live, but behave indiscriminately towards their mates and other males if they are presented on video (Swaddle et al. 2006). Male Anolis lizards are equally aggressive towards males of their own species and males of other species, but when these opponents are displayed on video male lizards aggress more towards the members of their own species (Macedonia et al. 1994). Female swordtail fish (Xiphophorus helleri) prefer males with long tails
to a greater extent if these males are shown on video than if the males are presented live (Trainor and Basolo 2000). In a related study by Friedman (1977), who notably conducted his research well before any real empirical and theoretical precedent was established, the growth of female ring dove’s (Streptopelia risoria) reproductive physiology was found to depend on the social contingency of her male partner’s behaviour. A single male dove was surrounded with six females whose visual access to the male was filtered by clear, one-way or opaque glass viewing panes. The results showed that the female viewing the male through clear glass had greater follicular development than the female that viewed the male through one-way glass, suggesting that social contingency may have affected the females’ physiological growth (Friedman 1977).

The contingency of a live partner’s visual signals are thought to help sustain a subject’s attention and social motivation, which, may function as bases for the formation of social preferences (Macedonia et al. 1994; D’eath and Dawkins 1996; Kodric-Brown and Nicoletto 1997; D’eath 1998; Fleishman and Endler 2000; Oliveira et al. 2000; Swaddle et al. 2006). Unfortunately, in every one of the experiments cited above, the manipulation of social contingency has been confounded either by the visual quality of the partner’s image, the partner’s behavioural content or the partner’s facing direction. On video, the image’s colour, depth and luminance may appear distorted. On video, the behaviour of the social partner is also not socially stimulated in the exact same way across live and playback conditions (Kodric-Brown and Nicoletto 1997). Often, the social partner presented on video is filmed at an angle that is different from the subject’s natural viewpoint during live interactions. Thus, the basic question of whether visual communication behaviour is intrinsically interactive remains unresolved. Nonetheless, these works are invaluable in that they have provoked questions about the meaning of social contingency and coherence within visual communications. It is becoming increasingly clear that scientists have only just begun to scratch the surface of these phenomena. Furthermore, if these findings are accurate - that social contingency somehow affects an animal’s ability to engage in
social preferences - the absence of social contingency in video playback stimuli could present a dangerous confound for video playback experiments. Studies varying such constructs as attractiveness, familiarity or social rank – where subject responses rely on their social preferences - may be seriously confounded by the lack of interaction available in the experiment. Thus not only is the present research important in furthering our basic understanding of communication, but understanding interactive behaviour is also vital in upholding the integrity, validity of video playback research as a whole.

1.3 Characteristics of visual communication

Understanding interactive behaviour in the visual channel is predicated upon understanding what social contingencies and social coherence look like in the visual domain. The following section lists some basic characteristics of the visual communication channel that may fundamentally shape social contingency and interactive behaviour.

1.3.1 Complexity

The biological motions characterizing actions, reactions, signals and gaits are the building blocks of visual communication. As a stimulus, the visual motion patterns of animal bodies are extraordinarily complex. How, exactly, biologically and psychologically relevant information is encoded in these patterns is not well understood (Troje 2002). Remarkably, the visual system has evolved to effectively detect and identify biological motions, including local level movements like movements of the head, feet, tail and wings (Mather et al. 1992; Troje and Westhoff 2006) and global level actions like postures, gaits and even movement ‘styles’ like male versus female, sick versus healthy, dominant versus subordinate, anxious versus relaxed and so on (Yamazaki et al. 2003; Troje, 2002). Each motion, action or style ‘category’ can be derived from their place in a complex ‘state space’ of non-rigid motions, which represents all possible variations of the motion’s dynamic trajectory, velocity profile, rhythm and spectral composition
(Troje 2002). For species which employ body movement in communication it can be assumed that their visual system is highly specialized to decompose and evaluate their own species specific biological motions.

While most work on biological motion perception has been carried out in humans, there is growing evidence that many non-human species possess visual systems specialized to extract information from their own species-typical motion patterns (Blake 1993; Watanabe et al. 1993; Shimizu 1998; Regolin et al. 2000; Tomonaga 2001; Goto et al. 2002; Yamazaki et al. 2003; Vallortigara 2006; Szafirski et al. 2007). For instance, young chicks prefer biological movement patterns just after hatching, a finding which implies an innate predisposition to detect and follow biologically moving objects (Regolin et al. 2000; Vallortigara et al. 2005; Johnson 2006; Vallortigara 2006). Such a predisposition could foster the development of visual processes specialized for their own species body movements (Johnson 2006).

Beyond the evaluation of a single conspecific’s movement, it has been speculated that the visual system may even identify biological motion profiles on an interactive level, extracting information about social contingencies to identify categories of interaction such as playing, fighting, chasing etc. (Blythe et al. 1999; Scholl and Tremoulet 2000). Considering the complexity of the movements in just a single animal, adding the dimension of social interaction yields a vast number of inter-individual contingencies: a highly complex stimulus for the visual system to process. For example, local movements, like wing or beak movements, may occur meaningfully in response to the vocal behaviour of a social partner (West, 1988; Williams, 2001; Todt, 1980). Also, movement patterns defining actions may be meaningfully related between animals, such as when birds take flight in near unison, feed or groom together, or copy the action strategies of conspecifics (Zentall 2004). Even the contingencies between movement ‘styles’, such as those that characterize fear, aggression or excitement (de Gelder et al. 2004), or
behavioural rhythms (Hanson et al. 1971; Aizawa 1998) appear to convey important information about the individuals participating in that group.

Whether or not non-human animals can evolve specialized visual skills to perceive the contingencies and coherence in social interaction, similar to the way in which the visual system has become specialized for perceiving a single conspecific’s complex movement, is a compelling, but perhaps far-fetched, possibility. To complicate the matter even further, individuals directly participating in the interaction - which is the type of interactive behaviour of concern in this thesis - cannot rely on the visual channel alone to access this information. Participants in social interactions must rely on their own kinaesthetic senses for retrieving information about the relations between their own behaviour and that of another animal.

1.3.2 The mirror problem

While perceiving a conspecific’s display is a visual task, the sense of one’s own self-produced body movements involves multiple sensory modalities. The sensations allowing animals to evaluate their own movements have been collectively termed the kinaesthetic senses, involving primarily 1) the sense of limb and body position (proprioception, somatosensory areas) and 2) the sense of motor effort (somatomotor areas) (Proske and Gandevia 2009). In other words, the social signals that individuals emit themselves and the social signals displayed by others are perceived and processed through highly disparate sense organs and channels in the brain. This quality will be referred to here as the mirror problem to describe the fundamental lack of correspondence between the visual and motor modalities used for sensing social contingency in the visual domain.

The mirror problem is unique to the visual communication channel. In vocal interactions, for instance, an individual’s own vocalizations and a partner’s vocalizations are both processed, at least in part, through the same auditory channels. In visual interactions, of course, the animal
cannot see itself in the same way it sees a social partner. Thus, the mirror problem has profound
and unique implications in the visual domain. For one, signal interference between self-produced
and other produced signals, which is a non-trivial problem in other communication modalities
(Brumm, 2006; DiPaolo, 2000) is not a major problem in the visual channel. An animal can
perform visual display simultaneously with the display of another animal without disrupting the
perception and processing of each other’s social signals, provided that their own display does not
obscure or block their view of the other animal. In contrast, auditory communication necessitates
some degree of social coherence, like turn-taking, simply to avoid the signal interference that
occurs during simultaneous vocal productions. In visual interaction, simultaneous mutual display
may therefore be characteristically common compared to other communication modalities,
because self-produced and other-produced signals do not interfere with each other during signal
transmission.

The mirror quality also imposes unique limitations and constraints on sensing patterns of
social contingency and, therefore, on any psychological processes that may drive interactive
behaviour in the visual domain. Compared to the simpler computational problem of comparing
self and other-generated behaviour within the same sensory domain, as in vocal-auditory signal
interactions, behavioural sensitivity to contingencies within visual communications could only
occur via cross-modal processing and would be uniquely constrained by the limits of their
connectivity.

1.3.3 Subtlety

Taken together, the complexity of biological motion and the mirror quality of visual
signal interactions creates the potential for producing perceptually subtle yet meaningful
contingency and coherence during interaction. For one, social contingencies and coherence can
be sparsely distributed within the interaction, where meaningful relations can occur between
many possible combinations of otherwise disparate local and global biological motion features. Thus, unless the visual system is specifically attuned to notice such contingencies, the untrained or unspecialized visual system (like that of a scientific observer) would have little chance at zoning in on behaviourally relevant contingencies. Also, due to the mirror quality, visual interactions may not require highly ritualized ‘macrostructure’, like turn-taking, to function efficiently, as do vocal interactions. Given the potential complexity of the social contingencies between visual signals, together with the lack of requirements for an organized back-and-forth dialogue, visual contingencies may be characteristically subtle. Meaningful social contingencies likely appear as brief instances temporal and spatial coincidences between two animals’ movements. Considering this potential subtlety, relevant social contingencies in visual interactions may only be identifiable by using either tightly controlled experimental tests for interactive behaviour or rigorous dyadic behavioural analysis.

In studies of human interaction, the measure of interactional synchrony (a type of social coherence) refers to degree of temporal coincidence between the boundaries of two interacting individuals’ body movements (Condon 1974; Condon and Ogston 1966). The measure captures a collection of what may appear individually as quite obscure events - like the movement of one person’s hand co-occurring with his partner’s head-tilt - but together add up to describe perceptually subtle, yet behaviourally meaningful pattern of social coordination (Bernieri 1988). Interactional synchrony has been measured between people conversing (Bernieri 1988; Bernieri et al. 1994; 1996), walking (Zivotofsky and Hausdorff 2007), idling (Richardson et al. 2007) and in romantic ‘dating’ scenarios (Grammer 1990; Grammer et al. 1998; Grammer et al. 2000). Although specific social contingencies are rarely noticed by interactants or observers of the interactions, people seem to have an ‘intuitive sense’ of their presence and degree. When participants are asked to evaluate their feeling of social ‘togetherness’ in the conversation their reports correlate closely with the measure of interactional synchrony. Interactional synchrony
also correlates with reports of social rapport (Bernieri 1988; Tickle-Degnen and Rosenthal 1990; Bernieri et al. 1994; Bernieri et al. 1996; Miles et al. 2009), sexual attraction (Grammer et al. 1998), satisfaction in relationships (Julien et al. 2000) and with measures of social attention (Macrae et al. 2008), mutual gains in negotiation (Maddux et al. 2008) and social attachment (Isabella and Belsky 1991). Interactional synchrony in humans provides a potentially characteristic example of how social interactivity in the visual channel might manifest in other species as well; producing social contingency and coherence that is extremely complex and subtle but nonetheless behaviourally and psychologically relevant.

1.4 Coordinated mutual display

*Coordinated mutual displays* are cooperative interactions in which social contingency and coherence is ritualized - exaggerated, stereotyped or repeated – and therefore appears to serve a signaling function (Malacarne 1991; Lorenz 1966). Evolutionary theory predicts that such displays evolve in species where 1) particular individuals tend to form relatively durable associations with each other and 2) these individuals stand to benefit from signaling/displaying cooperatively (Serpell 1981). Monogamy, in particular, represents a set of socio-ecological conditions which favour the evolution of coordinated mutual display. A mated pair engages in several types of mutual display behaviour like courtship, triumph ceremonies, nest relief, greetings and ritualized copulations, displays which can co-develop, co-adapt and co-evolve throughout the span of their pair bond (Wachtmeister and Enquist 2001; Di Paolo 2000). In some species, coordinated mutual displays exhibit a level of precision that goes unmatched by even many human performances. Scientists reserve the term duet for these extraordinary showcases of ritualized social coherence.

Duets are characterized by precisely timed and stereotyped mutual contingencies, occurring repeatedly and predictably in time, alternating or synchronizing between two
individuals (Wickler 1980; Langmore 2002; Hall 2003). The visual duet, also called *pas de deux* (French for ‘step of two’) (Huxley 1968), has evolved in 70+ species of mostly large migratory water birds that live in open habitats. These include members of *Anatidae* (ducks, geese, and swans), some gulls, auks, grebes, loons, penguins, albatrosses and cranes (Huxley 1968; Malacarne et al. 1991). Although visual duets are only rarely captured on film, the sophisticated coordination between two albatrosses, *Diomedeidae* (Pickering and Berrow 2001), the ‘weed-tossing’ dances of two Western Grebes, *Aechmophorus occidentalis* (Huxley 1968; Nuechterlein and Storer 1982), the diving displays of two loons, *Gavia immer* (Tate and Tate 1970) or the bouncing display flights of two Siberian cranes, *Grus leucogeranus* (Bragina and Beme 2010), once seen, are rarely forgotten.

Although duetting, strictly defined, is not the primary focus of this thesis work, the fact that visual duetting has evolved independently in many different species suggests that social contingencies in general, may be biologically, behaviourally and psychologically relevant across many social species, even when they in cases where extreme duetting behaviour has not evolved. It is only in rare socio-ecological circumstances that coordinated visual display evolve into the exaggerated patterns of duets; it will be argued below, that such extreme ritualization of social contingencies in duets may have more to do with the social context under which these signals have evolved rather than with the meaning of social contingency as a signal in itself.

An important concept in signal evolution is whether a signal has evolved in a context of social conflict or cooperation. In a seminal book chapter, Krebs and Dawkins (1984) compellingly argued that each of these contexts places an identifiable signature on the evolved form of the social signal: namely, in how *exaggerated* or *subtle* the signal will evolve to be. Competitive communications are when the signaler benefits more from signal transmission than the signal recipient does. This conflict gives rise to a co-evolution between sender and receiver that culminates loud and flashy ‘forceful’ signals. Cooperative communications, on the other
hand, where sender and recipient have mutual goals, afford the use of subtle low-cost signals. According to this reasoning, highly ritualized forms of coordinated structure, like in duets, likely arise out of conflict between signaler and receiver. In these cases, the receiver of the signal is likely be an outsider that threatened either the territory of the signaling pair or the stability of their pair bond. Conversely, barely noticeable social contingency and coherence might arise as a signal within a cooperative relationship between a pair of mates, or potential mates. In this case, the subtlety of the signal minimizes the costs of signaling and benefits both members of the pair (Krebs and Dawkins 1984).

Cooperative signaling interactions can give rise to ‘conspiratorial whispers’ between allies or ‘quiet understandings’ between mates and are ideal for concealing social affairs from competitors and predators and saving energy (Krebs and Dawkins 1984). Thus, meaningful contingencies and coherence within cooperative communications may commonly take on forms designed not to grab attention, but rather to conceal (from outside observers) an alliance unfolding between two individuals. For instance, this strategy would be ideal for courtship, where overly obvious cues indicating a building relationship between the pair might incite greater competition from other singles. As another example, subtle interactional synchronies that send a message of sexual interest would be ideal for concealing interactions that are leading up to extra pair copulations with another partner. Given just how diffuse the information contained in biological motion interactions can be, coherence between visual displays could, in theory, evolve to be virtually invisible to outside observers, but remain perceptually accessible to the members of the communicating pair. Since such signals could evolve to be very subtle, cooperative interactions may rely especially on the confirmation of mutual contingencies and the sense of ‘togetherness’ created therein.

Perhaps one of the most valuable contributions of Krebs and Dawkins’ (1984) chapter was to point out that the lack of exaggeration in a particular behaviour does not imply that the
behaviour is not an evolved communicative signal. Although cooperative interactive signals may be extremely hard to identify and study, we can gain clues about their form and function by looking at the features that become exaggerated in the ritualized form of these signals: visual duets. The temporal synchrony of mutual movement observed in visual duets may therefore be a meaningful feature in other types of interactions as well.

The purpose of this section is to point out that there may be signaling value in the non-exaggerated social contingency and coherence of mutual displays, similar to that of interactional synchrony in humans. Such cooperative interactive signaling behaviour may be widespread in animal species but remain completely unobserved by field biologists, precisely because the information within interactive signals has evolved to go unnoticed by outside observers. Although subtle signals may be difficult to identify and investigate, it is important that scientists do not neglect their importance. Perhaps most of the time there is no need for costly exaggerated signals.

After arguing that behaviourally and psychologically relevant social contingency may exist in subtle forms, the next question that arises is, what social function might these signals serve?

1.4.1 The function of coordinated mutual displays

At a very basic level, social interactivity would necessarily be designed to optimize signal transmission in communications. By joining another animal in reciprocal communication the individual is faced with the problem of managing its own signal transmission amidst the task of staying attentive to their partner’s display. One group of authors (Brumm and Slabbekoorn 2005; Brumm 2006; Brumm and Slater 2007) suggests that a major factor affecting the way birds sing is to mitigate signal interference. If song elements within a vocal duet overlap, partners are essentially jamming the transmission of each other’s signal. Songbirds adjust the temporal pattern
of their singing by singing in precise alternation to produce clear effective communications with minimal vocal overlap (Brumm 2006).

In mutual displays using visual signals, the communication is not constrained by signal interference. Instead, visual signals performed together in time might actually enhance signal transmission. For example, socially contingent visual displays that occur during the vocal interactions of songbirds appear to play a role in maintaining the pair’s mutual attention to each other’s song (Williams 2001; Todt and Fiebelkorn 1980; West and King 1988; Eales 1989; Otovic 2009). Actions like wing movements, beak aperture modulations, head movements, hops and short flights are often tightly synchronized with either a bird’s own acoustic events or with the acoustic behaviour of their social partner. Self-synchronized movements appear to be employed especially in noisy conditions, and are thought to enhance a bird’s own vocal signal by drawing the recipient’s visual attention (Otovic, 2009; Todt and Fiebelkorn 1980).

On the other hand, movements that are contingent to elements of the partner’s song structure are thought to signal the bird’s attention and motivation towards their partner’s song (Todt and Fiebelkorn 1980; West and King 1988; Eales 1989; Williams 2001). In spotted morning warblers (Cichladus guttatta) female wing beats often occur rhythmically and in coincidence with the pattern of her male partner’s vocalizations (Todt and Fiebelkorn 1980). Such signals may help the male recognize that the female is in fact listening to and engaged with his song performance. Thus, this type of socially contingent behaviour appears to function not only in optimizing signal transmission, but also in signaling information about the individual’s commitment to the communication.

In the study of duets, researchers have debated about the functional significance of one feature in particular, the most exaggerated feature: the temporal precision of alternating song elements (Thorpe 1963). Wickler (1980) suggested an explanation for this feature that fits with the many of the diverse functions suspected of duet behaviour. His coyness hypothesis proposes
that the temporal precision of social coherence reflects the time that the pair invests in practicing their duet, and therefore advertises information about the pair’s bond strength - their mutual commitment to one another - as well as the pair’s coalition quality - the pair’s ability to cooperate in defending against sexual and territorial competitors. This information is thought to be used in diverse social contexts for various pair functions, including continuous mutual mate assessment throughout the pair bond, mutual mate-guarding and joint territorial defense against (Hall 2000; Grafe and Bitz 2003; Hall 2003; Grafe and Bitz 2004; Marshall-Ball et al. 2006; Logue 2007; Hall and Peters 2008; Hall et al. 2009). Notice that many of these functions represent communications arising out of social conflict, supporting the idea presented in the previous section that ritualized duets may evolve specifically in conditions of communicative conflict.

There is growing support for Wickler’s coyness hypothesis in explaining the function of vocal duets. Although vocal duets are not the primary focus of this thesis, the insights achieved into the function of interactive behaviour in vocal communication provide interesting examples of how these processes might function in visual communications as well. In wren species (Malurus) and magpie larks (Grallina cyanoleuca), for instance, the temporal precision of duets improves with pair duration and correlates with time spent in close proximity (Logue 2007; Hall and Peters 2008; Hall and Magrath 2007). In the magpie lark, more precisely coordinated duets tend to provoke a stronger reaction from territorial intruders than less-coordinated duets (Hall and Magrath 2007). Thus, the authors of these studies surmise that coordinative precision signals the pair’s bond and coalition strength.

In the context of mate guarding and territorial defense, situations which can co-occur, the precision of an antbird pair’s duet (Hyposcnemis peruviana) has been shown to vary in a context-dependent and functionally specific manner (Tobias and Seddon 2009). In response to an intruding rival pair, the pair duets precisely with no overlap. However, when the same pair is presented with a solo female intruder, the pair’s duet becomes uncoordinated and full of
overlapping elements. This imprecision is thought to arise because the paired female, threatened by the intruding female rival, does not join her mate in precise song, but instead jams her partner’s song to prevent him from engaging in the sexual advances of the female rival. The male antbird responds by switching his song-type in the middle of the duet, apparently attempting to thwart his partner’s vocal interference (Tobias and Seddon 2009). In the tropical boubou (\textit{Laniarius aethiopicus}), when a mated pair is intruded upon by a single rival male, the mated male jams not the song of his female partner, but instead overlaps the song of the competitor male while simultaneously joining in duet with his female mate (Grafe and Bitz 2004). The male boubou’s strategy, unlike the female antbird’s strategy described above, prevents the intruder from usurping his female but also spares conflict between himself and his mate (Grafe and Bitz 2004). These examples suggest that the evolution of complex and abundant song types composing duets as well as the variation in duet precision may be largely explained by sex-specific and context-dependent strategies (Tobias and Seddon 2009).

Unlike vocal duetting, visual duetting usually diminishes in frequency after reproduction has occurred each season, which should not occur if visual duetting served a territorial function (Huxley 1968; Tate and Tate 1970; Sjölander and Ågren 1972; Nuechterlein and Storer 1982). Instead, visual duets are thought to be adapted for fast and strong pair-bonding, heavy mate guarding and quick reproductive synchrony demanded by a short breeding season, migratory lifestyle and strong predatory pressures in open habitats (Malacarne et al. 1991). A group of researchers working with ring doves have suggested that movement synchronies function to elicit reproductive synchrony between the developments of both individuals’ reproductive behaviour and physiology (especially the female’s physiological development for egg laying) (Lehrman 1965; Friedman 1977; Cheng 1992) synchrony is likely to be, for the most part, a cooperative function, it would follow that). Since reproductive subtle, cost-efficient signals are most likely evolve for this purpose (Krebs and Dawkins 1984). In the case of exaggerated visual duets, on the
other hand, these signals likely evolved in a situation of social conflict, in order to send a strong message of pair bond strength and coalition quality to be received by incoming sexual competitors.

1.5 Summary

The aim of this chapter was to argue that social contingencies in visual communication may be characteristically subtle but nonetheless meaningful. The synchronization between movements in visual duets gives clues to understanding which aspects of social interactivity in visual communications may be meaningful across all forms of visual communications, whether ritualized or not. For instance, Todt’s (1980) and Williams’ (2001) work provided evidence that, during interactions between male and female song birds, the female’s visual signals often temporally coincide with the vocal signals of her male partner. Similar female responses that have been observed in other bird species are commonly extremely subtle, often on the order of milliseconds, and appear to function in signaling the female’s attention and attraction towards the male’s song (Todt and Fiebelkorn 1980; West and King 1988; Eales 1989; Williams 2001). The function of signaling social commitment to a communication partner with quick and precise co-incident visual signals appears to generalize across many degrees of coordination, whether occurring in loosely organized interactions or highly organized visual duets.

It is safe to say that in the large majority of visual interactions, social contingency and coherence is not ritualized, but rather is extremely subtle and hard to measure, even for highly motivated scientists. But, can the animal subject detect the social contingency and coherence contained within its own social interactions? And, is this the primary mechanism by which social contingencies and coherence act to influence behaviour? Or, could there be other dynamical processes that might create interactive social behaviour, where such behaviour may simply be an ‘emergent’ non-functional consequence of the interaction dynamic? The next chapter addresses
these questions and presents a discussion about the mechanisms underlying interactive social behavior.
Chapter 2

Mechanisms of Interactive Behaviour

The pursuit of understanding how interactive behaviour happens in animals, is relatively unchartered territory, especially in the domain of visual interactions. How do the contingencies and coherence within social interactions act on the interacting individuals to influence their behaviour? One approach to this question is to construe social contingency as a ‘stimulus’ that can be perceived by the visual system. The visual system may suffice from an outside observer’s perspective; outsiders might perceive social contingency and coherence through the object recognition parts of the brain by evaluating whether group members appear as a perceptual ‘unit’ or not. Or, for outsiders, extracting information from others’ coordinated displays could be much simpler than this. In species where groups of males produce synchronous displays for instance, like in fireflies (*Photinus*) or waving crabs (*Ilyoplax pusilla*), female observers are thought to choose a single mate amidst the massive interaction by simply picking the leading male (Greenfield and Roizen 1993; Aizawa 1998). While an outside observer may use simple perceptual mechanisms to detect and use the information in the relations between signals, social agents that are directly involved in the interaction are faced with the mirror problem (see p.11). Understanding one’s own visual interactions is not a purely visual problem but rather requires the use of both visual and sensorimotor modalities.

There are two basic approaches to explaining how an animal’s behaviour might become interactive. The first is the existence of interactive psychological mechanisms. We use this term to refer to any mechanism that involves psychological – perceptual or cognitive systems - that have evolved specifically to extract information from the social contingencies and/or social coherence of social interaction. Interactive psychology has been most extensively articulated in the field of developmental psychology in research investigating an early-emerging sensitivity to
social contingency in human infants (Murray and Trevarthen 1985; Gergely and Watson 1999; Nadel et al. 1999; Gergely 2000). The work focused primarily around a single type of psychological mechanism: the individual’s ability to identify a partner’s behaviours as responses to their own (Watson 1966; 1985; Tarabulsy et al. 1996; Gergely 2000). Initially, the terms social contingency perception (Watson 1966; 1985) or social contingency detection (Tarabulsy, 1996) were most often used to refer this capacity: to detect partner responses as being related to one’s own behaviour. However, this wording is problematic since the name implies the use of a specific cognitive process, a contingency analysis, for detecting partner responses, when these mechanisms are clearly not yet that well understood. As an alternative, some authors adopted the term social contingency sensitivity as a more cautious reference to the same general mechanism for response detection (Bigelow 1999; Bigelow and DeCoste 2003; Striano et al. 2006). However this term is also problematic. There is a need to distinguish interactive psychology such as response detection (and possibly other, yet to be identified functions) from other types of processes that might also explain interactive behaviour (described below). In the present work we use the term response detection to refer to the previously discussed psychological mechanisms underlying an individual’s ability to identify whether a partner’s behaviour is occurring in response towards one’s own behaviour (Watson 1966; 1985; Tarabulsy et al. 1996; Gergely 2000). The term social contingency sensitivity is reserved as a more general term to refer to behaviour that discriminates between interactions that vary in social contingency; this term implies nothing about the mechanism or function of such a behavioural tendency.

The second approach to understanding interactive behaviour has been recently developed by dynamical systems theorists. Their works have described how interactive behaviour can arise from social dynamics alone, in the absence of psychological mechanisms for detecting social responses (Di Paolo et al. 2008; Auvray et al. 2009; Froese and Di Paolo 2010). Social dynamics can be conceived as defining a ‘system’ of social interaction, where each individual’s perceptual
and behavioural processes are components making up that system (Di Paolo et al. 2008; Wolpert 2003). Individual behaviour may be influenced by what Froese (2007) calls the ‘constitutive autonomy’ of the interaction process, where there exists a reciprocal dependency between the individual agents’ behaviour and the overall coordination dynamics of the interactive system. The mechanism that has been suggested to underlie the emergence of interactive behaviour is perceptual crossing, named to describe the event that two perceptual activities of the same nature simultaneously interact (as in the case of mutual touch or engaging in eye contact) (Di Paolo et al. 2008; Auvray et al. 2009). Perceptual crossing gives rise to a form of social coherence that depends on the perceptual crossing dynamic to persist and, at the same time, makes it more likely for that perceptual crossing dynamic to persist (Di Paolo et al. 2008; Auvray et al. 2009). In other words, perceptual crossing acts to create a feed-forward self-perpetuating dynamic which, of course, also influences the individual behavior composing the system.

These two classes of mechanisms for interactive behaviour – interactive psychology and social dynamics - will be described in more detail throughout the rest of this chapter. To start, it is important to note that, although these two sets of mechanisms are capable of creating interactive social behaviour independently with unique functional implications for each, should they co-exist in behaviour, they are likely to function in a highly interdependent fashion. This feature makes it particularly difficult to distinguish between them with behavioural experiments alone. However, the main difference between them is clear. Interactive psychology occurs within the ‘individual’ and describes specialized brain mechanisms that are designed for detecting and evaluating the inter-signal relations and using this information for adaptive behavioural functions. Social dynamic processes, on the other hand, may not serve a specific function, but rather interactive behaviour can naturally emerge from the ‘system’ of social interaction; at the individual (psychological) level, the interactive behaviour emerging from social dynamics may simply involve stimulus ‘release’ mechanisms that are not inherently ‘interactive’ in themselves.
2.1 Response detection

To date, only one type of interactive psychological mechanisms has been thoroughly and repeatedly discussed: response detection. It should be noted however, that there may be other types of interactive psychology that have yet to be considered, and we suggest one such mechanism in the conclusion of this thesis. For now, we review the literature on response detection.

Social contingency is valuable information, mainly because it indicates that a partner’s responses are causally linked to the individual’s own actions. Imagine a massive colony of noisy conspecifics with multiple individuals communicating at once. An animal that senses the relations between its own signals and the social responses that they trigger has immense potential for adaptively optimizing their social behaviour. Partner responses, once recognized can be used as social feedback: the process by which part of the social signal is returned to the signaler’s sensory system (via a response) in order to help regulate signaling behaviour (Wolpert 2003; Scott 2004). Social feedback processing allows the signaler to learn the consequences of their behaviour and how those consequences will vary depending on the social circumstance. Through learning, the animal can gain a rich understanding of their social environment as well as their own ability to influence it (Bigelow 2001; Marler 1997).

Just as ethologists work to understand what drives animal behaviour by testing subject reactions to various types of ‘sign-stimuli’, animals that use partner responses as feedback can ‘experiment’ with their own social behaviour to discover how their signals act in their social environment. Such animals can essentially act as natural psychologists, by modifying their own behaviour to gain an understanding of and control over their own behaviour and other animals’ responses to it (Krebs and Dawkins 1984; Wolpert et al. 2003).

Is it feasible that non-human animals have awareness about the causal connections between their own behaviour and that of another? Causality cannot be perceived directly but can
only be inferred from its perceptible correlates (Hume 1874; Michotte 1963). The available cues that together might enable animals to access the information in social response patterns include social contingency, as well as the temporal and spatial contiguities between contingent signals or other types of relational qualities linking signals to their responses (e.g. matching the type, form or intensity of signals) (Gergely and Watson 1999).

Once the animal is exposed to repeated pairings between their own signal and a partner’s response, they may be capable of learning the signal-response relationship. This results in the acquisition of an expectancy for that response, which becomes activated each time the animal performs that signal (Bolles 1972). This type of operant learning is thought to function similarly in any situation where behaviour is repeatedly followed by reward, animals tend to repeat behaviours that result in rewarding outcomes and discard behaviours that do not. In theory, whether a reward is food, water, shelter, or a reinforcing social signal, the mechanisms of learning expectancies through feedback are the same (Bolles 1972; Marler 1997; Wolpert 2003).

Although the specific neural-cognitive mechanisms for contingency detection are not well understood (Balleine and Dickinson 1998; Dickinson and Balleine 2000b), it is generally agreed that social contingency analysis is especially demanding (Porr 1998; Watson 1985; Chadwick-Jones 1991; Bigelow 1999). This is because social contingencies, such as a response to a signal, as compared to physical contingencies, such as an object hitting another object and causing it to move, are characterized by high levels of variability and noise. To demonstrate this mathematically, one can assign a contingency coefficient between 0 and 1 describing the conditional probability of the relationship (Watson 1966; Gergely and Watson 1999). Physical contingencies are generally characterized by perfect contingency coefficients of 1 (Michotte 1963). Social contingencies are characterized by high yet imperfect contingency coefficients typically between 0.7 and 0.9 (Bigelow 1999). Social responses are also variably delayed in time and have unpredictable forms and dynamical outcomes, as compared to the consequences of
mechanical actions which can usually be defined by a finite set of variables and physical laws. As Moran (1992) aptly pointed out, the existence of contingency is a necessary, but not sufficient, condition for causality and therefore contingency is not a perfect indicator of social responsiveness. In the noisy conditions of the social domain, the error rate of response detection using contingency analyses alone could be relatively high.

Social contingency analysis, if used, is likely most important when an animal initially learns a social response expectancy. After an individual acquires a response expectancy however, it may be most efficient to supplement contingency analysis with other, more accessible, information that cue social responsiveness (Gergely Watson 1999; Scholl and Tremoulet 2000). Heuristics are mechanisms that make use of low-level features to identify complex phenomenon (Blythe et al. 1999; Scholl and Tremoulet 2000; Michotte 1963). There are a number of low-level consistencies between signals and responses that could be used as useful heuristics for inferring partner responsiveness. As already noted, these include timing, spacing and the relative type, form or intensity between a signal and its response (Gergely and Watson 1999). Such heuristics would almost certainly involve multisensory mechanisms; the individual must relate some type of motor-related activity (kinaesthetic sensations) associated with their own signaling behaviour with the visual activity associated with their partner’s signals.

As a simple example, if an individual waves to a friend and the friend waves back promptly, the second wave is quickly perceived as a response. However, if the individual waves and the friend, instead, starts to yell and thrash about, the timing is right but both the intensity and the form of the response are mismatched with respect to signaler’s expectation of their friend’s response behaviour. This situation would leave the signaler very confused as to whether the friend’s actions were in response to his well-meaning gesture, because in the signaler’s learned experience in using a wave, yelling is not an expected response.
In the scenario described above, if the respondent’s yelling and thrashing was actually in response to some other event, say, getting stung by a bee immediately after the signaler waved, this random temporal coincidence would explain the apparently bizarre response. The prompt temporal succession, or *temporal contiguity*, between behaviours is commonly used by signalers to identify a partner’s responses. And indeed, while it is effective for the most part, this simple heuristic can easily lead to an erroneous sense of social responsiveness. Recently, Miller and colleagues (2009) demonstrated that marmoset (*Callithrix jacchus*) contact calling interactions may be sustained by sensitivities to the temporal contiguity between calls. Using interactive audio playback techniques, they showed that a monkey is most likely to answer another monkey’s contact calls if its partner’s call occurred within 3s of the monkey’s initial signal. Therefore, the timing of the conspecific’s response behaviour appears to bestow a calling monkey with a sense of its partner’s responsiveness (Miller et al. 2009). The temporal properties of responsiveness may be consistent across different animal species and across different types of signal-response relations since sensory-motor transformations triggering responses are likely to constitute evolutionarily old, conserved mechanisms. Heuristics for exploiting the temporal consistencies between signals and responses therefore, could conceivably also constitute evolutionarily old, conserved mechanisms for response detection across social species.

In the spatial domain, species capable of appreciating another animal’s line of sight (Hampton 1994; Wavve et al. 2002) may use this information to infer social responsiveness. For instance a scrub jay (*Aphelocoma coerulescens*) will re-bury its food stash in another location if a potential pilferer is seen observing the jay’s stashing behaviour (Clayton et al. 2007). Similarly, the piping plover (*Charadrius melodus*) performs an injury feigning display at the sight of a predator’s gaze, but goes about its daily business as soon as the predator turns its body and eye-gaze away from the plover (Ristau 1991). Such instances imply that these species form an expectation about the observer’s responsiveness, e.g. that a potential pilferer will steal food or
that a predator will attack, based on the relation between their own behaviour and the other animal’s facing direction. It is also possible that cues of spatial contiguity, like the proximity and relations between the dynamic trajectories of two animal’s motion paths help animals to discern the nature of their social relations. Both pigeons and humans have been shown to discriminate relative motion paths between dots on a screen, depending on whether those dots move in a trajectory consistent with coherent group dynamics like a wolf chasing sheep or move randomly (Goto et al. 2002; Blythe et al. 1999). The proximity between two interacting individuals may also be taken as a cue indicating the nature of a response; approach or distancing behaviour could help identify the quality of a response as aggressive, submissive or sexually interested depending on the social context.

2.1.1 Response detection in humans

The ability to detect social responses has been most extensively investigated in human infants to understand how and when these capacities develop (Murray and Trevarthen 1985; Hains and Muir 1996; Muir and Hains 1999; Nadel et al. 1999; Striano et al. 2006). To test for the infant’s ability to detect social responses, scientists have infants interact with their mothers over a double closed-loop teleprompter interface (see p.4). This setup gives both mother and child the experience of being engaged in a natural, real-time (Live) social interaction with each other. To test response detection, part way through the communication the video feed seamlessly switches so that the infants suddenly view a pre-recorded video (Playback) of their mothers. Given that the only difference between the Live and Playback conditions is the presence of social contingency in the former and its absence in the latter, any differences in the infants’ behaviour has been taken as evidence for their learn expectancy for their mother’s social responses (Trevarthen and Aitken 2001). However, as will be explained later, the validity of this conclusion has recently been brought into question (Auvray et al. 2009).
To gain a sense of what the closed-loop teleprompter interface experiment tests, consider if the Live and Playback conditions were run on adults human subjects. Indeed, if vocal communication was included in the experiment, an adult in the Playback condition would quickly identify that their partner’s speech does not relate properly to their own side of the conversation. However, if the experiment was restricted to visual interactions, it is not entirely obvious that a human adult would immediately recognize the absence of responsiveness in their partner’s non-verbal behaviours, unless the participants were given explicit instructions to check for partner responsiveness. Although this experiment has not been done with human adults, it would be interesting to examine a participant’s response detection abilities in an unstructured, ‘idle’ visual interaction and to discover what behavioural contingencies are noticed and remembered and what strategies participants adopt to check for social responsiveness using only body language and facial expression.

Human adults tend to interpret and verbally report social experiences as a series of causally linked events (Tenenbaum and Griffiths 2003), forming expectations about other people’s responses and reflecting on social behaviour when these social expectations are violated. The relatively new but rapidly growing field of social neuroscience provides insight into the human capacity to understand others' actions, intentions, beliefs and desires and to share and experience the feelings of others (Gallese 2001). Researchers have explained these processes with various operational constructs, like ‘theory of mind’ (Gallese and Goldman 1998; Vogeley et al. 2001; Siegal and Varley 2002; Saxe and Kanwisher 2003), the action-perception manifold (Knoblich and Sebanz 2006; Sebanz et al. 2006) or theory-based causal reasoning also known as ‘theory-theory’ (Tenenbaum and Griffiths 2003). Although people’s understanding of others’ behaviour as responses to their own would be expected to be an important point of discussion in this literature, discussions about the role of social response detection in social behaviour are surprisingly few. A notable exception is Daniel Wolpert’s (2003) account of how the brain works
during social interaction to control social behaviour. He conceptualizes that the areas of the brain that plan and execute social behaviour are, essentially, a specialized extension of the motor control system. This analogy implies that the computational function of the brain is the same whether a person is controlling their actions for grasping the handle of a coffee cup, manipulating a screwdriver or sending out a social signal. In social interaction the endpoint or ‘effector’ of the motor control system is the other person’s social behaviour, akin to the grasp of one’s fingers around the coffee cup in motor control, or the tool’s movement in tool use. The brain controls behaviour by storing ‘internal models’ of the environment in the motor system. These internal models code the consequences of actions, whether those consequences occur in the actor’s fingers, a tool they are holding or another person they are communicating with. Implicit in this framework is that detecting social responses is a critical aspect of controlling social behaviour in social interaction. The user constantly predicts, evaluates and matches actual social responses against those that were predicted by the model, just like the motor system does when reaching for a cup of coffee. For example, if, when lifting the coffee cup, it doesn’t budge, the motor system updates the internal model of the coffee cup (e.g. the cup is heavier than expected) and recalibrates the motor system to manage the extra load. Similarly, if, when sending out a social signal, the recipient doesn’t respond, the motor system re-evaluates the internal model (e.g. the recipient has bad eyesight) and re-calibrates social behaviour to manage the receiver’s bad vision (e.g. by increasing the amplitude, speed and frequency of the signal). Thus in Wolpert’s (2003) framework, social responses are constantly being detected, predicted and used for controlling social behaviour. This control system design is conceived to be a fundamental characteristic of the brain systems managing any motor behaviour, whether the goals of that behaviour are social or mechanical.
2.1.2 Response detection in animals

While the human’s ability to detect social responses is rarely disputed and often taken for granted, authors are exceptionally cautious about attributing this ability to animal species, and rightfully so. However, the idea that animals are capable of causal reasoning and, in particular that this capacity is specialized for the social domain, is becoming increasingly accepted (Premack and Premack 1994; Cheney et al. 1995; Kummer 1995; Byrne and Whiten 1998; Dickinson and Balleine 2000a; Dickinson and Balleine 2000; Zuberbuhler 2000; Emery and Clayton 2004; O’Connell and Dunbar 2005; Blaisdell et al. 2006; Hauser and Spaulding 2006).

Given the close evolutionary relationship between humans and other primates, the field of social cognition has primarily focused on primate species (Premack and Premack 1994; Cheney et al. 1995; Zuberbuhler 2000; O’Connell and Dunbar 2005; Hauser and Spaulding 2006). To give just one example of the clever experiments conducted in this field, Cheney and Seyfarth (1980) filmed three Vervet monkey mothers (*Chlorocebus pygerythrus*) side-by-side, while playing a recording of one of the female’s two-year-old offspring screaming. When the audio tape played, the mother of the juvenile looked and approached the location of the scream, while the other two females reliably looked towards the mother (often before she moved) indicating that they expected the mother to respond to her offspring’s calls (Cheney and Seyfarth 1980).

The study of social cognition in non-primate species has taken the approach of demonstrating that social behaviour is extremely flexible; animals tend to modify their alarm calling, food-referencing, sexual or territorial behaviour depending on variations in their own signaling abilities, the characteristics of their social partner and the composition of the social ‘audience’ surrounding them (Craig 1908; Evans and Marler 1991; Evans and Marler 1992; Pepperberg 1994; Marler and Evans 1996; Bravery and Goldizen 2007; Can et al. 2007; Hoover and Robinson 2007; Smith and Evans 2009; Kokolakis et al. 2010). For instance, the food referencing behaviour of male fowl (*Gallus gallus*) is sensitive to the male’s social rank and the
composition of the social audience (Smith, 2009; Evans, 1994). If only a female is present the male will reference food items frequently and loudly with vocalizations, but will do so silently with ‘tidbiditting’ gestures if other males are around, particularly if these males are more dominant than the subject (Evans, 1994; Smith, 2009).

Many researchers studying such flexible context-dependent social behaviour believe that it can be most clearly explained, not by a very extensive and complicated set of and stimulus-dependent response mechanisms (which would require an enormous brain to store) but rather by the animal’s ability to learn and control behaviour by registering social consequences in relation to their own actions (Marler and Evans 1996; Emery and Clayton 2004; Zentall 2004; Emery 2006). Supporters of this view believe that animals are in control of their social behaviour rather than being ‘slaves’ in their reactions towards social stimuli (Marler and Evans 1996).

2.1.2.1 Learning

Another line of evidence for response detection abilities in animals is in research showing that, for young animals to properly learn the signal repertoire of their parents or neighbors, they require live social interaction to do so. In songbirds for instance, merely hearing a tutor’s song without being able to reciprocally interact with them does not suffice for proper song development (Payne 1981; Baptista and Petrinovich 1984; Eales 1989; Beecher and Burt 2004). According to some authors, juvenile songbirds shape their innate songs into a region specific repertoire by detecting their tutor’s contingent response behaviour and using it as feedback (Beecher, 2004; West, 2008; Goldstein et al. 2003; Marler and Nelson 1993; Nelson and Marler 1994; King et al. 2005). Other authors suggest that tutor responses enhance learning by increasing the juvenile’s attention and arousal thereby emphasizing the saliency of certain behaviours over others (Ten Cate et al. 1992; Houx and ten Cate 1999). Whatever the specific mechanism is,
learning seems to occur because juveniles tend to repeat behaviours that elicit favorable social responses and discard behaviours that do not (Nelson and Marler 1994; Marler 1997).

Perhaps surprisingly, several studies have identified visual feedback as a preeminent factor in song-learning interactions (Adret 1997; Bolhuis et al. 1999; Eales, 1989; Hultsch et al. 1999; Beecher and Burt 2004). Eales (1989) found that 10 out of 11 zebra finches (Taeniopygia guttata) that could interact visually and vocally with a tutor learned their tutor’s song completely. However, only 3 out of 7 juveniles learning song from a live but visually isolated vocal tutor interaction copied the tutor’s song. Similarly, Payne and Pagel (2001) caged young Indigo Buntings (Passerina cyanea) with two male tutors, one that was able to interact both visually and vocally and another that could only interact with the juvenile vocally. The young buntings learned only the song of the adult male that they could interact with visually and did not learn the song of the unseen male (Payne and Pagel 2001). Apparently even a human experimenter can serve as a visual tutor for enhanced song learning in nightingales (Luscinia megarhynchos): when a familiar experimenter visually interacted with the juveniles during tape-tutoring, the juveniles learned the song pattern more completely and perfectly compared to birds that were exposed to the tape only (Todt et al. 1979). Even an arbitrary visual stimulus, a flash of light, enhanced song learning in nightingales, as long as these stimuli were displayed in a temporally co-incident manner with to the correct version of the song (Hultsch et al. 1999).

The study of juvenile Cowbirds, Molothrus ater ater, has provided particularly outstanding evidence for the role of visual cues in song learning (West et al. 1981; King and West 1983; King and West 1988). A young male housed alone with an adult female develops a song dialect consistent with the female’s native song preference. This finding came as a surprise to the researchers since female cowbirds do not sing. To investigate, West & King (1988) videotaped interactions between young males and an adult female. The videotapes revealed a very subtle female visual signal that co-occurred with the male’s song: a rapid 200 ms wing-stroke action.
Although these wing strokes happened infrequently, about once for every 100 songs produced, the researchers were able to show that juveniles retained the song material that elicited the wing stroke response. Later in the male’s development, songs associated with wing strokes were significantly more potent and effective as courtship signals, which West and King (1988) measured by copulatory responses in females.

Learning, of course, is not restricted to juveniles but can continue throughout adult life (Nottebohm 1981). Each time an individual experiences changes in their social life – e.g. a new mate, a new territory, new neighbors, a new social rank or a loss in signaling abilities - there is a need for developing new social behaviour (e.g. Bravery and Goldizen 2007). For instance, mated pairs of duetting birds co-develop a unique duet repertoire which improves constantly throughout their pair bond (Hall, 2008). Furthermore, visual cues appear to play a special role even in adult song development. In whitethroats, *Sylvia communis*, for instance, males increase songs that elicit rapid female hops from female mates (Balsby and Dabelsteen 2002). In zebra finches also, males increase their courtship display depending on visual feedback from their female partner (Royle and Pike 2010). In bower birds (*Ptilonorhynchus violaceus*), female startling gestures act to reduce male courtship intensity and crouching signals increase male display. A re-occurring theme of these studies is that *female signals* appear to act to elicit modulations of the male’s sexual advertisement. Such communications are thought to benefit both male and female by increasing the efficacy of the females’ mate search as well as the male’s courtship efforts, by reducing the likelihood that the female will become startled and promoting situation appropriate and functionally effective sexual display in males (Patricelli et al. 2002; 2004; 2006). Thus, females and males that are capable of learning to improve their communication strategies will achieve more efficient courtship behaviour and better reproductive success throughout their lifetime (Patricelli et al. 2002).
The use of social responses as social feedback is becoming increasingly accepted as a mechanism shaping flexible and plastic social behaviour (Goldstein et al. 2003). The studies reviewed here provide powerful evidence for an early emerging ability to detect visual responses and to use these cues to shape adaptive behaviour. Whether a juvenile is cognitively aware of a partner’s responses (Nelson and Marler 1994; Marler 1997) or whether enhanced learning during social interaction emerges due to the dynamics of social attention and arousal (Ten Cate et al. 1992; Houx and ten Cate 1999) remains unresolved. In either case, the main conclusion here is the same. Any social behaviour which employs social responses as social feedback for guiding new behaviour implies that each signal fundamentally gathers its meaning from other signals preceding and following it. And, that behaviour is much more sophisticated than a set of stimulus-driven reactions, but rather, functions interactively and in a flexible and controlled manner.

2.2 Social Dynamics

To conclude that an animal has the capacity to use social responses as feedback is a claim with profound implications and should be cautiously examined. Even simple mechanical objects can produce complex patterns of coordinated behaviour as long as there is some mechanism of mutual influence. Two pendulums mounted together on the same beam, for example, create a system of forces that interact to synchronize the pendulums’ motions. As systems become more complex, as in social interaction, mutual influence can create interactive behaviour that may appear intentional but may actually be explained by simple dynamics (Scholl and Tremoulet 2000). Even as scientific researchers, striving to uphold a standard of objectivity, it can be difficult to escape the natural human tendency to over-attribute intentionality in its absence (Scholl, 2000).
In the early 1950’s W. Walter (1950) designed two robots ‘Elmer and Elsie’ that were programmed to explore their environment using circular trajectories and searching for moderate light. Each robot had its own light mounted at its sensory surface. The circuitry worked such that when a robot came in contact with a moderate light it moved towards it. By approaching, the light intensity hitting the robot’s sensory surface increased. When the intensity reached a certain level, the robot’s own light turned off for a short period. When Elmer and Elsie were placed in a room together, their interaction produced some fantastical coordinated patterns. Elmer and Elsie appeared to be dancing! They circled in exploration and upon mutually detecting each other’s light source, moved towards each other until a certain point where both their light sources simultaneously turned off and then both robots resumed their circling behaviour. After turning their lights back on, the robots would repeat this cycle, over and over again. The interaction process gained a ‘life of its own’; it acquired a kind of autonomy (De Jaegher and Di Paolo 2007; Walter 1950).

Elmer and Elsie were clearly incapable of social response detection. Although the interactivity of their behaviour was not specifically evaluated, their behaviour could be classed as interactive but in the absence of any interactive psychology for assessing the relations between signals. Clearly, then, one must be cautious about attributing complex cognitive mechanisms like response detection to organisms exhibiting interactive social behaviour. Elmer and Elsie’s coordination emerged from the fact that both robots had mutually attuned sensory behaviour and congruent behavioural reactions. Auvray et al. and Froese and Di Paolo (2008, 2010), have called this dynamic perceptual crossing: when two sensory experiences (in this case sensing each other’s light) of the same nature simultaneously interact they can produce a congruent pattern of mutual responsiveness that increases the opportunity for future sensory interaction (increasing future contact). Could these same dynamical processes be responsible for behavioural sensitivity to social contingency observed in human or animal subjects also?
Are human adults, for instance, actually ‘aware’ of a partner’s social agency during social interactions and is this awareness necessary for interactive behaviour to occur? To investigate this question, Auvray and colleagues (2009) used a minimalist systems approach: stripping social interaction down to only the minimal conditions required to observe the influence of social contingency on behaviour. They created a one-dimensional tactile virtual environment within which human adult participants could interact with each other by controlling an avatar (a virtual character) with the finger of one hand while receiving tactile feedback about the objects in the environment on their other hand. Another participant was simultaneously present in the same virtual environment and completing the same task. Each participant’s goal was to seek ‘social’ contact with the other participant and report, by a button press, when he believed he was interacting with the avatar of the other participant. Each participant could also run into a control stimulus, a spatially offset ‘shadow’ of the partner’s avatar which was therefore identical in motion patterns to the partner’s avatar but behaved in a non-contingent fashion. In this case identifying ‘social agency’ could be only be achieved by evaluating the relations between the behaviours of the two avatars. In this way, the partner’s live avatar and its shadow decoy were analogous to the Live and Playback conditions used to assess social contingency detection between infants and their mothers engaged in complex visual communications (see p.4) (Murray and Trevarthen 1985; Hains and Muir 1996; Muir and Hains 1999; Nadel et al. 1999). In light of the conclusions drawn from the studies in infants – namely, that infants discriminating between Live and Playback conditions necessarily identified partner responses and used them as social feedback - Auvray’s findings were quite profound. The participants could not consciously identify the difference between the partner’s avatar and its shadow, they reported ‘social agency’ in both stimuli with equal frequency.

Despite the inability to detect and identify ‘social agency’, the participants’ avatars’ spent significantly more time in contact with each other than they did with the motion-identical shadow
stimuli. The mechanism suggested to underlie these effects is the same that explains Elmer and Elsie’s interactive tendencies: perceptual crossing (Di Paolo et al. 2008; Auvray et al. 2009; Froese and Di Paolo 2010; Asada et al. 2008). When participants’ perceptual behaviour ‘crossed’ (i.e. when they both felt each other’s avatar) this event triggered congruent searching strategies in an attempt to maintain contact (oscillating finger movements). In the ensuing dynamic, the participants’ avatars oscillate around each other sustaining contact between them. The shadow object, of course, did not perceptually ‘cross’ with the participant and therefore instead of engaging in the interaction, the shadow object eventually lost contact and moved on. By aligning two agents’ perceptual and behavioural processes in time and space, perceptual crossing creates coherent and self-perpetuating social dynamics. These dynamics constitute and therefore influence each interactant’s social behaviour (Di Paolo et al. 2008; Auvray et al. 2009). As such, perceptual crossing can drive interactive social behaviour.

Although the minimal virtual environment approach has many limitations concerning its generalizability to complex social interactions, Auvray et al. (2009), as well as a number of computer simulation studies that followed (Di Paolo et al. 2008; Froese and Di Paolo 2010; Froese and Di Paolo 2008; De Jaegher and Di Paolo 2009; Asada et al. 2008) have produced conclusive demonstrations that a psychological capacity for social response detection is not a necessary condition for behavioural sensitivity to social contingency to emerge. Instead, interactive behaviour can be a naturally emergent property of social dynamics.

The influence of perceptual crossing on social behaviour is a newly articulated concept which happens to change the interpretations of multiple previous works. For instance, in the original experiments showing behavioural sensitivity to social contingency in human infants (e.g. Murray and Trevarthen 1985; Nadel et al. 1999), the attribution of cognitive response detection abilities to infants may not have been necessary to explain the effects of the experiments (Di Paolo et al. 2008; Auvray et al. 2009). Also affected, are the interpretations of many animal
behaviour experiments finding effects of social contingency on behaviour (e.g. Miller et al. 2009; Friedman 1977; Ord and Evans 2002; Royle and Pike 2010; Harcourt et al. 2009; Rosenthal et al. 1996).

2.3 Comparing interactive psychology with social dynamics

It is now understood that interactive behaviour can arise from psychological mechanisms alone, social dynamical mechanisms alone or both mechanisms working interdependently. The defining difference between these mechanisms is the level at which the processes underlying interactive behaviour exist. Interactive behaviour can derive from mechanisms at the ‘individual level’, meaning that the animal possesses specialized psychological capacities designed to evaluate the relations between social signals (such as response detection). Or, interactive behaviour can arise from mechanisms occurring at the ‘systems level’. The system encompasses the behaviour and perception of both animals, as well as the interactions between them (such as perceptual crossing). The interactive behaviour can only be understood by investigating the social dynamic system as a whole, the mechanisms involved cannot explained at the individual level alone.

Interactive psychological mechanisms define specialized mechanisms in the brain that are capable of relating the animal’s sense of self-action with the visual experience of seeing another animal’s actions. In discussing such mechanisms, many authors use language to imply that a subjective ‘awareness’ may accompany the subject’s sense that their partner’s behaviour is related to their own (e.g. Watson 2001, Friedman 1977). However, such ‘awareness’ should not be considered a necessary characteristic of interactive psychology. Interactive psychology does not necessarily imply conscious awareness; the animal’s ‘sense’ of social relations could function unconsciously as well. For example, when humans are asked to judge the ‘togetherness’ or rapport in their communications, their ratings accurately reflect measures of inter-individual
synchrony. But, people are not typically aware of every slight causal relation between their own behaviour and that of their partner. Rather, people appear to possess an intuitive ‘sense’ of their own social dynamics and do not seem to be aware of this sense unless explicitly asked to report it.

Social dynamics, on the other hand, explain the emergence of interactive behaviour in the absence of psychological mechanisms that are ‘interactive’. Interactive social dynamics are not ‘in’ the brain per se, but rather exist in the larger ‘system’ that is made up of the brain and behaviour of both animals. The underlying neural mechanisms involved can be as simple as visuo-motor reflexes producing reactive behaviour. Indeed, these visuo-motor reflexes have a psychological/neural basis, but those mechanisms are not, in and of themselves, responsible for interactive behaviour. Only if the individual, along with his visuo-motor reflexes, is placed in a system involving another individual with similar visuo-motor reflexes, does the whole system of social interaction become interactive. In such cases, the psychology of the single individual is not, by itself, responsible for the interactive behaviour observed.

The distinction between interactive psychology and social dynamics is perhaps most clear with regards to evolution and function. Interactive psychological mechanisms, if present, have almost certainly evolved to serve an adaptive behavioural function. An animal that is capable of sensing social coherence or detecting partner responses could use this information for evaluating social interactions, making decisions based on those evaluations and learning to optimize behaviour and its outcomes. This cannot necessarily be said of interactive behaviour emerging from social dynamics. It can happen spontaneously, as an emergent property of the interaction, even between two mechanical objects such as swinging pendulums. It is possible, however, that certain social dynamics are beneficial to the individual and others are detrimental and, as a consequence, individual behaviour has evolved (in the context of the social dynamic) to increase or reduce certain interactive dynamics. This sort of evolution may or may not involve interactive psychology. Such evolutionary pressure might act to change visuo-motor reflexes alone or it
could also promote the evolution interactive psychology that exploits the informative, predictable influence that social dynamics have on behaviour. Similarly, social dynamics could become dramatically influenced by the animal’s sense of the interaction dynamic; if individuals are equipped to interactively adjust their behavioural patterns based on inter-signal relations, this would in turn change the interactive behaviour of the social dynamic as a whole.

An experimenter investigating interactive social behaviour is faced with a number of challenges. Even once a perfectly controlled and realistic experimental paradigm is achieved and the experimenter has demonstrated that social behaviour is interactive, the problem of distinguishing between the mechanisms that underlie that behaviour requires new consideration. In the next chapter, we explore the potential for using a closed-loop teleprompter interface for investigating interactive social behaviour. Although, ultimately, one cannot make a satisfactory distinction between psychological and dynamical mechanisms using this experimental paradigm alone, we explore the extent to which this paradigm can help identify potentially relevant social contingencies and perceptual crossing events in social interaction. Before presenting the experiments, the chapter begins by introducing our animal model, the pigeon.
3.1 Introduction

Compared to the striking visual duets of some species, the mutual display of two pigeons is quite unspectacular. Their interaction has no obvious exaggerated, stereotyped or repeated patterns of social contingency and the degree to which their displays reciprocally influence one another is not entirely clear. Studying social interactivity in ‘unspectacular’ mutual displays, like those of pigeons, is important for achieving basic insights about the entire spectrum of coordinated visual displays, all of which likely evolved from an original ‘unspectacular’ form.

Contrary to common first impressions, pigeon social behaviour is sophisticated and complex. A well-known ethologist, Wallace Craig, who along with Lorenz formulated some of the foundational concepts of ethology, employed the pigeon as a primary model in his life’s work. He argued that the flexibility of social behaviour generated during this animal’s lifetime cannot merely be the result of social reflexes but rather should be described as a chain of variable, striving, goal-directed responses (appetitive behaviour), which terminate in the performance of a simple stereotyped response (consummatory act) (Craig 1918). Wallace suggests that ‘no internal machinery, no system of instincts be it ever so perfect, could carry an individual dove through the vicissitudes to social life without the agency of social control’ (Craig, p.87). The debate over whether animal behaviour is governed purely by stimulus-release mechanisms or by controlled, intentional, goal-seeking cognition is one that is active in ethology today. Craig’s ideas still govern one side of this debate. In using such language like ‘social control,’ ‘striving’ and ‘goal-directed responses’ Craig argues for capacities in the dove that rely on the ability to sense another animal’s responses as being related to their own.
3.1.1 The circle walk

The circle walk is a staple in the pigeon’s social life; it is a visually ‘loud’, complex, flexible and multifunctional display (Goodwin 1983). Its dynamic ‘style’ distinctly includes bowing and cooing, rhythmic postural changes, fast charging paces and, as the name implies, a circular walking path. The variations in these features cater the display to a variety of sexual, assertive and defensive social situations (Goodwin 1983). The walking trajectory, for instance, is not always a perfect circle but rather appears highly variable across different individuals and contexts, sometimes occurring in half circles, figure eights or “T” shapes.

Divergent evolutionary pressures have shaped distinct male and female versions of circle walking behaviour. The male circle walk is considerably more aggressive than that of females. Male pigeons are more likely to chase, charge and peck other birds, and perform a dramatic bow-coo action, inflating their exaggerated vocal sac while concurrently calling with a boisterous vocal coo (Fabricius and Jansson 1963; Goodwin 1983). The female’s display is more subtle. Female circles are less often complete, but commonly consist of partial turns, and the bow-coo is also less distinct. Occasionally the female runs forward with her head down, fanning and dragging her tail feathers. Quick head nodding movements are also commonly observed in the pauses between a female's circles (Goodwin 1983).

3.1.2 Social interactivity in the pigeon

The mechanisms that govern a pigeon’s social reactions and responses will ultimately define the pattern of social contingencies and coherence that occur between two interacting partners. Merely seeing the image of a conspecific can trigger circle walking in subjects and this response becomes greatly enhanced when the conspecific is seen moving (Frost et al. 1998; Shimizu 1998; Partan et al. 2005). Shimizu (1998) suggests that the influence of social motion cues on subject responses may be explained by the presence of social-triggers that are
intrinsically dynamic, or, by the influence of movement in grabbing the subject’s attention towards socially relevant cues. In either case, the works of Frost et al. (1998), Shimizu (1998) and Partan et al. (2005) have shown that a pigeon’s circle walking display has an ongoing dependence on the dynamic features of conspecific display.

To date, a handful of studies reveal mixed results about whether pigeons behave interactively. When Shimizu (1998) presented male pigeons with female stimuli presented either live, across clear glass or on video, the male courted both females with equal vigour, suggesting that the pigeon is not sensitive to the social contingency or coherence present in the interaction. On the other hand, in another study with the same experimental conditions, this time measuring the male pigeon’s brain activity, the subject’s brain appeared to ‘behave interactively’ (Patton et al. 2009). The gene expression in ‘visual association areas’ depended on whether the male interacted with either socially contingent or non-contingent females. It is important to note that in both studies (Shimizu 1998; Patton et al. 2009) the experimental manipulation of social contingency was confounded with the visual quality of the female stimulus (distorted on video) as well as in the presence of female vocalizations (present only in live interactions).

In a similar vein, Friedman’s (1977) study showing ‘interactive reproductive physiology’ in female ring doves (see p. 8) also provides evidence for social contingency sensitivity on a physiological level in a close relative of the pigeon. Thus, so far, there is evidence that a pigeon’s brain and physiology discriminate between socially contingent and non-contingent partners (Friedman 1977; Patton et al. 2009), whereas interactive courtship behaviour has yet to be observed (Shimizu 1998).

In a different type of experimental paradigm, Toda and Watanabe (2008) investigated the pigeon’s ability to sense the temporal contiguity of contingencies between their own behaviour and a video of themselves streamed live. Their experiment tested the bird’s ability to discriminate both real-time contingent (Live) self-video and delayed contingent (Delayed) self-video from
non-contingent pre-recorded playbacks of self-video (Playback). Although the stimuli were video presentations of self, the task was similar to that of detecting responsiveness in a social situation, like in a typical video playback experiment. In both cases, the subject must assess the relations between his own motor behaviour and that of a pigeon displayed on screen. It is possible that self-images were identified by subjects not as an image of self, but as a conspecific (Toda and Watanabe 2008). The pigeons were trained first to discriminate between the Live self-images and Playback self-images. The ability to learn this initial discrimination showed that subjects discriminate between a temporally contiguous self-image stimuli and non-contingent self-image. The subjects were able to transfer this learning to discriminate between Delayed self-images and Playback self-images, scoring higher than chance even when their self-images were delayed by intervals of 7 s (Toda and Watanabe 2008). The pigeon’s discrimination performance necessarily required psychological mechanisms for comparing their sense of self-action with their visual perception of a dynamic ‘social’ stimulus: an ability which characterizes the presence of interactive psychology.

3.1.3 Introduction to the experiments

The evidence gathered to date gives a sorted answer to the question: do pigeons behave interactively? On the one hand, in a relatively natural social setting, pigeon behaviour appears robust to the experimental distortion of social contingency in courtship; yet, on the other hand, the pigeon’s brain activity actually appears to pick up on these abnormalities (Shimizu 1998; Patton et al. 2003). In a more controlled but less natural ‘social interaction’, where the pigeon is rewarded for detecting the temporal contiguities between their own behaviour and a video of themselves streamed live, they appear highly adept at discriminating videos based on contiguous ‘social’ contingencies alone (Toda and Watanabe 2008).
In the following experiments we use a controlled experimental design – the closed loop teleprompter interface - to examine whether pigeons behave interactively in visual communications. With this setup, the pigeons’ behaviour in a natural real-time social interaction (Live) can be compared with their responses towards a previously recorded social partner (Playback). Since the Playback condition is recorded during the pairs corresponding Live interactions, the stimuli are identical except for the presence of absence of social contingency.

Four experiments and one post hoc analysis are presented. Experiment 1 explores methods for quantifying pigeon behaviour and introduces an automated technique for coding circle walking behaviour with motion energy analysis. Experiment 2 tests whether pigeon courtship can be classified as interactive, by comparing the pigeon’s response towards a social partner presented Live or in Playback conditions. Experiment 3 tests whether social interactivity relies on cues present in the facing direction of partner display; by moving the teleprompter camera 90° away from its original location, the partner display is manipulated to appear as if it is directed 90° away from the subject. Experiment 4 tests whether social interactivity depends on social timing and social context. Three time delays, 1s, 3s and 9s were chosen to approximate the duration of visual signals in the pigeon’s behavioural repertoire (the bow, the circle and the circle walking bout, respectively) and to manipulate the temporal contiguity of social contingency. Both opposite sex and same sex pairs were studied to investigate whether social-context affects social contingency sensitivity. Lastly, a post hoc dyadic analysis of the data collected in Experiment 4 is used to test the role that two specific social contingencies may play in the pigeon’s interactive behaviour: 1) the act of responding to circle walking with circle walking and 2) the event of simultaneous circle walking.
3.2 General Methods

3.2.1 Subjects and housing

A total of 9 male and 9 female homing pigeons (*Columba livia*) were selected from a pigeon aviary in the psychology animal laboratory of Queen’s University. The housing aviary, 23 m², contains a colony of 70 pigeons assembled from racing breeders in the Ontario area. Birds were selected to participate in the present studies if they exhibited active courtship behaviour in the aviary and maintained it under experimental conditions inside the teleprompter apparatus. During the course of experiments, subjects were socially isolated; they had auditory and olfactory but no visual access to other birds in the room. Subjects were housed individually in standard steel rabbit cages (60 x 46 x 40 cm) and kept on a feed of cracked corn and standard pigeon grains. Their light cycle was kept such that it approximated the City of Kingston natural dawn-dusk light cycle. In the winter months their light cycle was adjusted to speed up their moulting process. Experiments never took place while the birds were moulting. The experiments took place between February 2005 - May 2006 (Experiment 1), April - August 2008 (Experiment 2), August - November 2009 (Experiment 3) and December 2009 – January 2010 (Experiment 4).

3.2.2 Apparatus

A double closed-circuit teleprompter apparatus was used to allow two birds separated in different rooms to interact naturally in real-time (Figure 1). This apparatus used two teleprompters to enable live social interaction over a video interface, allowing each subject to be filmed from a hidden camera placed behind the live video image of the other subject. Each pigeon was placed in a 46 x 46 x 46 cm thin steel frame cage with walls made of mist netting. In front of each subject’s cage was the teleprompter apparatus which housed a video monitor, a half-silvered mirror and a video camera. The video image of a conspecific was displayed on the 19” Samsung LCD Syncmaster 1701 monitor lying flat and projecting upward onto the half-silvered mirror (64
(50 x 55 cm) oriented 45° to the monitor and 45 ° to the plane of the subject bird’s visual field. Directly behind the half-silvered mirror was a Sony Handycam video camera (frame rate: 30 fps interlaced) fixed so that it pointed vertically downwards inside the teleprompter, filming the subject bird at eye level by way of a small mirror placed a few inches below the camera (45° to the camera and 45° to the bird). The purpose of this mirror was to compensate for the mirror flip that occurs on the half-silvered glass when the video image is projected. The teleprompter apparatus was housed in a steel frame (60 cm wide x 64 cm tall x 67 cm long). To make the interior of the teleprompter dark, black Choroplast plastic board was used to cover the top and the sides of the teleprompter apparatus. This ensured that the subject bird saw only the reflection of the other bird on the half-silvered mirror and could not see any of the interior of the teleprompter where the video camera was housed. The same black plastic board was also used as a background placed behind each subject as it was being filmed. The camera and teleprompter were calibrated to make the visual image of the stimulus bird life-sized, so that it appeared to each subject that its partner was present directly in front of him/her. The final image was projected approximately 60 cm away from each pigeon, as measured at eye level from the centre of the subject’s cage to the half-silvered mirror.

An additional observation camera was placed in each room to get a clean video record for behavioural coding and analysis. The output from all four cameras fed into a central computer in a third room where the experimenter observed and recorded experimental trials with security camera software. The video from the camera in the teleprompter apparatus was recorded with a Digital Video Recorder which recording high quality uncompressed footage of the Live to use in the Playback condition. Time delays for Experiment 4 were produced with Prime Image D1 Pipeline, Audio/Video Delay Synchronizer with Digital I/O.
Figure 1. The double closed-loop teleprompter apparatus.

Two teleprompters enable live social interaction over a video interface, allowing each subject to be filmed from a hidden camera placed behind the live video image of the other subject. Black dotted and long-dash grey lines denote the course of visual information flow through the video channel from one bird to the other in either direction. The video camera inside the teleprompter films one pigeon off a mirror and through a pane of one-way glass. The video then streams into the control room where the experimenter can control and manipulate the experimental stimuli, and then into the teleprompter apparatus of the other subject. Two surveillance cameras, used to collect data for behavioural analysis, are not depicted in the diagram.

Figure 2. A male pigeon courting a female partner displayed live in the teleprompter apparatus.
3.2.3 General Procedure

Before the experiments began, birds were habituated to the experimental apparatus for 30 minutes daily until they appeared comfortable and responded with visual display to videos of conspecifics. During a typical experimental trial two birds were placed in separate rooms, each containing a teleprompter apparatus. At trial onset the monitors were switched on in the teleprompter apparatus of both birds simultaneously. No bird was run more than once every 4 hours and experiments always took place between 8 am and 6 pm. No audio communication between birds was available and ‘babbling brook’ sounds from a radio alarm clock were used to mask the pigeons’ vocalizations during the experiment trials.

3.3 Experiment 1: Coding pigeon courtship behaviour

Coding visual communication behaviour for analysis can be conducted in various ways. Most researchers use some type of manual coding, which entails watching the video collected from each experimental trial, counting and recording the behaviours of interest. The main behaviours of interest here are the dynamic visual signals composing courtship display which can include circle walking, bowing, cooing, and tail dragging and preening. Circle walking is particularly ideal for evaluating both male and female courtship behaviour, since, out of all the other signals in courtship it appears most consistently in both sexes (Goodwin 1983).

An alternative to manual coding is to use the dynamic quality of visual signals to develop a method for automatically coding behaviour. On video, animal movement translates into measurable motion energy. When the pigeon circle walks, for instance, the motion energy values obtained from video are elevated with respect to the motion energy values obtained when the pigeon is not circle walking. This affords the ability to automatically code circle walking behaviour by using an algorithm which measures motion energy in video footage. Automatic coding has obvious benefits. It drastically reduces the time required for coding behaviour and
reduces human error. It also makes it very easy to view the data as a time series, using any size
time scale the researcher desires. Here, we test the validity of using motion energy analysis for
automatically coding circle walking behaviour by comparing circle walking data obtained from
the automatic coding method with that obtained from the method of coding the behaviour
manually.

3.3.1 Methods

3.3.1.1 Materials

To compare coding techniques we present data from an experiment in 2006 which we
will refer to here as Experiment 0 (Ware and Troje 2007). Experiment 0 investigated social
interactivity in the pigeon by manipulating the presence and timing of social contingency in a
partner’s display. In Experiment 0, six male and six female pigeons were paired in every possible
combination to yield 36 pairs of birds. The five experimental conditions consisted of social
interactions over the double closed-loop teleprompter interface where the partner was presented
either in real-time (Live), delayed by 1s, 3s or 9s, or as a recording taken from the Live condition
(Playback). Each pair underwent all five conditions in two minute trials. Two experimental
blocks were completed to create a total of 360 trials.

About a year after Experiment 0 was conducted, an error in procedure was discovered
that had severely confounded the original experimental question. The experimenter had used two
different video camera settings to collect the footage that was displayed to the subject. The Live
condition was recorded to tape and used as the stimulus in the Playback condition. The time
delay conditions were recorded to camera memory and streamed directly to the display in the
subject’s teleprompter apparatus. It was later understood that these two camera settings recorded
with different frame rates. Recording to tape produced video that was 30 fps interlaced (60
fields/s) while recording to camera memory produced video that was 15 fps progressive (15
frames/s). In interlaced video, each frame is displayed as two consecutive fields, where each field contains every second line of a new image. In progressive video the whole image frame is presented.

While this error completely invalidated the data from Experiment 0 for answering the original experimental question, the data set was still useful. First, the data is used here to determine the validity of an automatic method of coding behaviour. Second, once the experimental confound was discovered the data revealed that pigeon courtship behaviour is highly sensitive to the frame rate of the video on which conspecific stimuli are displayed. This led to a valuable discussion about the influence of motion perception on animal responses towards video playback stimuli.

Due to the error described above, the experimental conditions can be fully described by variations in frame rate as well as by variations in social contingency. Considering these two factors together, the five conditions are best labeled as C1. L-30fps, C2. 1s-15fps, C3. 3s-15fps, C4. 9s-15fps and C5. P-30fps (L = Live, P = Playback).

3.3.1.2 Manual Scoring

The pigeon behaviours coded manually include circle walking, standing, walking, coos, bows, tail drags and preens. Circle walking, standing and walking were quantified by their duration. Coos, bows, tail drags and preens were all quantified by their frequency. In bowing, the bird lowers its head to the point where its beak is near a right angle to the ground and the iridescent display plumage on the lower part of the neck becomes enlarged as the bird produces a simultaneous coo (Goodwin 1983; Troje et al. 1998; McGraw 2004). The coo accompanies the bowing display in a stereotypically synchronized fashion and has been described as sounding like ‘oo-roo-c’too-coo’ (Baptista and Abs 1983). Tail draging, the spreading and lowering of the tail feathers, is thought to be an element of driving behaviour which is commonly used by males to
drive females away from competitors and towards his nest site (Fabricius and Jansson 1963). The courtship preen is thought to be a displacement behavior occurring when a drive, like mating, is left unable to be fulfilled (Goodwin 1983). Circle walking, which was described in detail on p.45, was coded only if the bird completed a full 360° circle or figure eight. If the bird stopped for at least 3s and then restarted circle walking, a new circle walking bout was coded. See Table 1 for a description of the behaviour that was coded in the present study.

The Queen’s Video Coder Software (Baron et al., 2001) was used to code the frequency of behavioural events and the duration of behavioural states. This coding software allows the coder to register the occurrence of behaviours as they occur in the video. All vocal behaviour was counted from the visually displayed audio waveform in Sony Sound Forge. There were four raters in total, the experimenter and 3 undergraduate volunteers. Raters were always blind to experimental condition. The raters were all trained by the experimenter and practiced coding using a pilot video clip before analyzing test trials. Each video was rated by at least two raters yielding an average inter-rater reliability of 86% for the total scores of all behaviours tested.

<table>
<thead>
<tr>
<th>Display States</th>
<th>Display Signals</th>
</tr>
</thead>
<tbody>
<tr>
<td>Circle walking: Circle walking is coded when the bird completes a full 360 degree circle or figure eight. Stopping within circle walking bouts was coded only if the bird was stationary for 3s or more.</td>
<td>Head bow: Thrusting the head and neck forward and below the body of the bird.</td>
</tr>
<tr>
<td>Walking: Walking without display.</td>
<td>Coo: A vocalization characterized by a biphase waveform:</td>
</tr>
<tr>
<td>Standing: Remaining stationary.</td>
<td>Tail Drags: Fanning and lowering the tail feathers.</td>
</tr>
<tr>
<td></td>
<td>Preen: The bird touches its beak to its feathers on the back, the breast or the tail.</td>
</tr>
</tbody>
</table>

Table 1. Manually coded pigeon courtship behaviours
3.3.1.3 Automatic Coding

The motion energy in the videos was measured using optical flow analysis algorithms embedded in the EyesWeb Open Software Platform Motion Analysis Library (Camurri et al. 2004). This software is available for download at www.eyeweb.org. The EyesWeb procedure first converts the video to gray scale, and then computes a value for the vertical and horizontal optical flow at each position in the image over each frame transition, using the Lucas–Kanade method for image registration (Lucas and Kanade 1981). The matrix of optical flow values are squared and averaged, producing a single motion energy value for each frame transition. Thus, for each 2 minute 30 fps video processed, this procedure output a data series containing 3600 motion energy values, one for each frame transition in the video.

The time series of motion energy for each video was smoothed and filtered in Matlab. Smoothing averages the data over a window of consecutive data points to remove noisy fluctuations in the motion energy data. The threshold that is used for filtering the data approximates the motion energy value that is achieved only if the subject is performing the specific behaviour of interest, in this case, circle walking behaviour. In order to identify the motion energy threshold that delineates a target behaviour, the researcher must manually locate time points in the video where the subject performs that behaviour and match these time points to a graphical display of the motion energy data. This comparison allows the researcher to identify the boundary delineating the motion energy values obtained while the animal is at rest from the motion energy values produced while the animal performs the display. The value identified at this boundary becomes the threshold used for automatic coding. To investigate pigeon circle walking behaviour we used a smoothing kernel of 23 frames (averaging over a window spanning the 11 preceding frames and the 11 following frames for each individual value) and a threshold of 3 (motion energy). The duration of circle walking was taken as the total number of frames in which the motion energy values are above the threshold of 3. The duration of frames above threshold
was then converted to time above threshold in seconds, to yield a final automatically coded measure of circle walking duration, referred to here as *motion energy above threshold* (s). Motion energy above threshold (s) can then be compared to the manually coded measure of circle walking duration (s).

3.3.1.4 Analysis

A Pearson correlation coefficient was computed to assess the relationship between the measures of motion energy above threshold (s), circle walking duration (s), number of bows, number of coos, number of tail drags, standing (s), walking (s) and number of preens. An alpha value of .01 was used to evaluate significance, \( n = 360 \).

To evaluate whether both methods of coding circle walking behaviour would produce similar results in an experimental analysis, both the motion energy above threshold (s) dataset and the circle walking duration (s) dataset were analyzed with a two-way repeated measures ANOVA, \([\text{condition (5) x sex (2)}]\) using an alpha value of .05 to evaluate significance. Condition is treated as a within subjects factor, sex is treated as a between subjects factor and the subject is treated as the random variable \( (N = 12) \). Pairwise t-tests were used to compare the L-30fps condition with each of the other four conditions, where a Bonferroni corrected alpha value of .0125 is used to assess significance.

3.3.2 Results and discussion

There was a strong positive correlation between the measures of motion energy above threshold (s) and circle walking duration (s), \( r(358) = .936, p < .01 \). A scatterplot summarizes this result (Figure 3). Overall, these two measures of circle walking behaviour (motion energy above threshold and manually coded circle walking) correlated positively with bowing, cooing and tail dragging and correlated negatively with standing, walking and preening. The correlation coefficients are summarized in Table 2.
There is a strong positive correlation between the automatically coded measure of motion energy above threshold (s) and the manually coded scores of circle walking duration (s). Motion energy above threshold represents a measure of circle walking duration. This measure is obtained by quantifying the motion energy of behaviour captured on video.

Figure 3. The correlation between motion energy above threshold and circle walking duration
Table 2. The relationships between measures of courtship behaviour

<table>
<thead>
<tr>
<th></th>
<th>Motion Energy</th>
<th>Circle walk</th>
<th>Bow</th>
<th>Coo</th>
<th>Tail Drag</th>
<th>Stand</th>
<th>Walk</th>
<th>Preen</th>
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<tbody>
<tr>
<td>Motion Energy</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Circle Walk</td>
<td>936**</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>Bow</td>
<td>724**</td>
<td>708**</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Coo</td>
<td>603**</td>
<td>609**</td>
<td>801**</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Tail Drag</td>
<td>589**</td>
<td>560**</td>
<td>.498**</td>
<td>.490**</td>
<td>1</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Stand</td>
<td>-.924**</td>
<td>-.956**</td>
<td>-.739**</td>
<td>-.616**</td>
<td>-.571**</td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Walk</td>
<td>-.008</td>
<td>.003</td>
<td>-.071</td>
<td>-.083</td>
<td>-.061</td>
<td>-.009</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>Preen</td>
<td>-.480**</td>
<td>-.458**</td>
<td>-.444**</td>
<td>-.329**</td>
<td>-.268**</td>
<td>.552**</td>
<td>-.103</td>
<td>1</td>
</tr>
</tbody>
</table>

Correlations between the measures of motion energy above threshold (s), the duration of circle walking (s), number of bows, number of coos, number of tail drags, the duration of standing (s), the duration of walking (s) and the number of preens are listed in the table. Motion energy above threshold represents a measure of circle walking duration. This measure is obtained by quantifying the motion energy of behaviour captured on video and identifying a threshold in motion energy which indicates the subject’s performance of circle walking behaviour. All the other behavioural measures were obtained with manual coding methods. The double asterisk (**) indicates significance at the 0.01 level.

The results of the ANOVAs show that the effect of condition on circle walking behaviour are similar whether the measure of motion energy above threshold (s) or the measure of circle walking duration (s) is used. The effect of condition on behaviour is significant in the data obtained from both methods of coding behaviour (motion energy above threshold (s) $F(4, 40) = 6.84, p < .001$, manual coded circle walking $F(4, 40) = 8.64, p < .001$). Differences between conditions were also found to be similar whether the data was automatically coded (C1 vs. C2, $t(11) = 3.29, p = .009$, C1 vs. C3, $t(11) = 3.43, p = .006$, C1 vs. C4, $t(11) = 3.37, p = .007$) or
manually coded (C1 vs. C2, $t (11) = 2.94, p = .015$. C1 vs. C3, $t (11) = 3.44, p = .006$, C1 vs. C4, $t (11) = 3.47, p = .005$). These results are shown in Figure 4.

Figure 4. A comparison between manual coding and automatic coding with motion energy analysis.

The results of Experiment 0, where the duration of circle walking behavior was measured with two different behaviour coding methods, manual coding (dark bars) and automatic motion energy analysis (light bars). The graph shows that these two coding methods yield similar experimental effects on each measure of circle walking duration. Experiment 0 was originally designed to study the effect of social contingency on pigeon courtship behaviour. Due to human error, the effect of social contingency on pigeon courtship behaviour was confounded by differences in frame rate. The Live and Playback conditions were displayed to the subject at 30 fps interlaced and the time delay conditions (1s, 3s, and 9s) were displayed at 15 fps progressive. The resulting conditions are C1. L-30fps, C2. 1s-15fps, C3. 3s-15fps C4. 9s-15fps and C5. P-30fps (L = Live, P = Playback). The asterisk (*) in the figure denotes significant differences between the marked condition and the L-30fps condition.

The results show that automatically coding social behaviour using motion energy analysis yielded valid experimental data which correlates closely with manually coded scores of circle walking behaviour. After setup, the EyesWeb motion energy analysis ran on its own, and the data can be acquired within a few days. When this method was used here to measure circle walking behaviour in pigeons, the data showed similar experimental results to those achieved with manually coded data. The data also show that the circle walk is a satisfactory measure of
pigeon courtship intensity: this behaviour correlates closely with other behavioural measures of courtship intensity, like bows, coos and tail drags, it can be easily quantified with automatic motion energy analysis and provides a useful measure of the courtship intensity for both male and female birds. For the rest of the experiments presented, we used motion energy analysis for coding the pigeon’s circle walking behaviour from video. For simplicity, the measures obtained from automatic coding will be referred to as circle walking behaviour from here on in; even though the measure is more accurately labeled as motion energy above threshold.

3.4 Experiment 2: Testing for interactive behaviour in courtship

Throughout three decades of video playback research investigating visual communication in animals, several authors have noted that subject behaviour differs in response to conspecifics presented on video as compared to conspecifics presented live (Macedonia et al. 1994; Kodric-Brown and Nicoletto 1997; D’eath 1998; Fleishman and Endler 2000; Oliveira et al. 2000; Swaddle et al. 2006). The animals’ sensitivity to social contingency is one of many possible explanations for this observation, since there are multiple differences between a video image of a partner and a real partner presented live (see p.6). The possibility that pigeon behaviour is sensitive to social contingency has received mixed support (see p.45) (Friedman 1977; Shimizu 1998; Toda and Watanabe 2008; Patton et al. 2009). In fact, there have been no perfectly controlled tests of behavioural sensitivity to social contingency in any non-human species. The present experiment tests the existence of interactive behaviour in pigeons with a controlled experimental design using the double closed-loop teleprompter apparatus. Since the pigeon experiences a socio-sexual ecology that is associated with highly coordinated visual duetting behaviour in other bird species (Malacarne et al. 1991; Todt and Naguib 2000; Patricelli et al. 2006), it is predicted that pigeons will show behavioural sensitivity to social contingency during courtship.
3.4.1 Methods

3.4.1.1 Subjects and stimuli

Six male and six female pigeons were paired in every possible opposite-sex combination to yield 36 pairs of birds. A Live and Playback condition were used to manipulate social contingency in courtship interactions (see p.48). The Live condition is a video mediated real-time interaction which supports the formation of natural social contingencies between the subject and its partner. In the Playback condition, the subject views a video playback of the same partner, the recording of which was obtained from the video camera located inside the teleprompter apparatus during the pair’s Live condition. The composition, sequence and intensity of the partner’s social behaviour is identical across the Live and Playback conditions, the only difference is the subject’s capacity for social influence which is necessary to establish social contingency.

3.4.1.2 Experimental design

Each trial contained six minutes of social interaction, split into three, two minute segments and each segment was interspersed by a one minute wait period. The reason for using this stimulus-on, stimulus-off procedure was to stimulate as much circle walking interaction as possible since birds tend to behave more intensely at stimulus onset.

Each pigeon experienced both conditions with six different partners. For half of the 36 pairs, the female acted as the subject and the male was the social partner, i.e. the male was filmed during the Live condition to create footage which acted as the Playback stimulus for the female subject. For the other 18 pairs, the male acted as the subject. Thus, every pigeon acted as a subject three times (with three different partners) in each experimental condition, yielding 72 trials. This design was run twice for a total of 144 experimental trials. In the second round the subject-partner roles for each experimental pair were switched.
3.4.1.3 Behavioural measures

Circle walking behaviour was coded using automatic motion energy analysis (Experiment 1). The time series of circle walking data was processed to represent circle walking behaviour in three ways: 1) total circle walking duration, 2) average bout duration and 3) number of circle walking bouts. Although these measures are all related to one another, their pattern is informative. Total circle walking duration gives an overall measure of display behaviour, while the latter two measures provide information about the pattern of the circle walking display.

3.4.1.4 Analysis

We conducted three 2-way, [2 (sex) x 2 (contingency)] repeated measure ANOVAs, where sex is a between-subjects factor, contingency is a within-subject factor and the subject was treated as the random variable. The three ANOVAs correspond to the three measures of circle walking behaviour – total circle walking duration, average bout duration and number of bouts. Main effects were evaluated using an alpha level of .05 (N = 12).

3.4.2 Results

The results revealed a main effect of social contingency but no interaction between sex and contingency, on circle walking behaviour. In both sexes the pigeon’s total circle walking duration and average bout duration varied significantly (F (1, 10) = 6.864, p = .026, F (1, 10) = 10.47, p = .009, respectively) across the Live and Playback conditions (Figure 5). There was no effect of social contingency on the number of circle walking bouts.

The results also reveal a main effect of sex on circle walking behaviour, where males exhibited longer average bout durations (F (1, 10) = 8.53, p = .015) and fewer bouts (F (1, 10) = 536.52, p < .001) than females (Figure 6). There was no effect of sex on total bout duration.
Figure 5. Circle walking behaviour across Live and Playback conditions

Pigeons’ total circle walking duration and average bout duration varied significantly depending on whether their social partner was displayed Live in the teleprompter apparatus or displayed as a Playback of the previously captured footage (recorded during the Live condition). Within each pair, the partner’s behavior was identical across the Live and Playback condition, the only difference between conditions was the presence or absence of contingent partner responses towards the subject. The asterisks (※) denote significant differences (p < 0.05) between the behavior occurring in the Live conditions and the behavior occurring in Playback conditions. These findings suggest that pigeon circle walking can be classified as interactive behavior.

Figure 6. Sex differences in circle walking behaviour

Male and female pigeons each have distinct patterns of circle walking behavior. Males exhibit long circle walking bouts lasting on average 7 seconds, whereas females exhibit much shorter but more frequent circle walking bouts lasting only 3s on average. Significant differences between male and female circle walking are indicated by the asterisk (※) over the female data point, p < 0.05.
3.4.3 Discussion

The findings show that pigeons behave interactively in courtship; circle walking is not governed solely by the visual signals immediately preceding it, but also by the social contingencies existing between signals. The results also demonstrate sex differences in circle walking. Males circle in long bouts, while females tend to circle in shorter but more frequent circle walking bouts.

Unlike previous methods used for testing the influence of social contingency on behaviour (Friedman 1977; Kodric-Brown and Nicoletto 1997; Trainor and Basolo 2000) the present study manipulated social contingency in isolation while controlling all other aspects of the social stimulus, including the colour, depth, motion, luminance and behavioural content of the partners’ image. In using a controlled experimental design, the findings greatly substantiate other researchers’ concerns about the lack of interaction available in video playback experiments (Kodric-Brown and Nicoletto 1997; Trainor and Basolo 2000; Swaddle et al. 2006; D’eath and Dawkins 1996). The inability of the subject to interact with a partner presented on video should indeed be considered a complex and dangerous confound in experiments using video playback.

The present results contrast with previous tests of the social contingency sensitivity in the pigeon. Shimizu (1998) and Patton et al. (2009) did not find significant differences in male pigeon courtship behaviour towards females presented either live (across a pane of glass) or on video playback. There are a few methodological differences that might explain this discrepancy.

First, instead of using circle walking duration to operationalize courtship intensity, Shimizu (1998) and Patton (2009) measured the frequency of discrete behavioural signals like coos, tail drags and bowing. These behaviours are correlated with circle walking behaviour (Experiment 1); however, the exact nature of the relationship between them and circle walking is not entirely clear. The circle walk might be considered as a ‘dynamic scaffolding’ in courtship, providing a structure for other discrete signals to be transmitted in an organized and efficient
manner. If circle walking plays a direct role in organizing and maintaining coherent communications between two interacting animals, circle walking may exhibit greater sensitivity to the manipulation of social contingency than other discrete behavioural measures.

The second major methodological difference between this study and previous work is the length of the experimental trial used. Shimizu (1998) and Patton et al. (2009) both measured behaviour during two minute interactions and the present study measured behaviour across six minutes of interaction. During pilot work for the present investigations, the trial duration was increased from two minutes to six minutes for an experiment with mixed condition trials (e.g. Live-Playback-Live, Playback-Live-Playback, Live-Live-Live), designed to control for stimulus familiarity effects (Ware, unpublished, Hains and Muir 1996). Although this complex design did not turn out to be the best for investigating social contingency sensitivity in pigeons, it was clear from looking at the data that the six minute trial duration increased the sensitivity of the experimental assay to the effects of social contingency on behaviour, leading us to use six minute trial durations for the present study. The increase in social contingency sensitivity over time can be seen in Figure 7.
Total circle walking duration is shown over three, two minute trial segments. It can be seen that the difference in behavioural responses towards the Live and Playback stimuli increases as the trial proceeds.

While the length of the trial may seem like a trivial detail, in the study of interactive behaviour it may be a critical methodological factor. As social interaction proceeds, courtship behaviour becomes progressively sporadic and less predictable. Later in the trial, birds frequently stop circling for chunks of time and then spontaneously re-initiate the display, which sometimes triggers partner behaviour but not always. Early in the trial, behaviour is more vigorous, automatic and ‘reactive’. Therefore early courtship behaviour might represent a ceiling with respect to the effects of social contingency on behaviour. This is especially true in experimental settings where a) socially deprived subjects are very ‘eager’ to engage in circle walking interactions, b) the highly controlled experimental context promotes predictable, regular, stereotyped responses and c) the precise controls on the stimuli produce a general pattern of social contingencies that would create a highly convincing ‘illusion’ of partner responsiveness and natural social coherence. In the span of two minutes, the pigeon’s behavioural sensitivity to

![Figure 7. Behaviour exhibits greater sensitivity to social contingency as the trial proceeds](image-url)

the difference in behavioural responses towards the Live and Playback stimuli increases as the trial proceeds.
social contingency sensitivities may not easily discriminate between a responsive and a non-responsive partner. It seems logical that if social contingency functions to sustain the duration of social engagements by maintaining the subject’s social attention and social motivation, as previously suggested by other researchers (Trainor and Basolo 2000; Swaddle et al. 2006), behaviour during the later stages of the social encounter might depend more highly on social contingencies than behaviour observed in the early stages of the interaction.

A helpful anecdotal analogy from human behaviour is the practice of recording a stereotypical and falsely ‘responsive’ voicemail greeting. If the recording is scripted carefully, the caller might engage in conversation with such a message for a considerable period of time before realizing that the voice on the telephone is in fact pre-recorded. Inevitably, the clue that uncovers the illusion is that the dialogue violates the caller’s expectations of his friend’s responsiveness and its natural timing, resulting in nonsensical response sequences, interruptions and abnormally long silences (Manning et al. 2000). Like in human conversation, pigeons might engage in ritualized visual dialogue as a ‘greeting’ which gradually becomes increasingly improvised and unpredictable, relying more so on reciprocal response structure to give each signal within the communication meaningful context. Six minute trials allow ample time for a natural decline in the stereotypy of behaviour to occur, and at some point, possibly after the male’s first circle walking bout, which often continues for a whole minute or more, the illusion of partner responsiveness declines and discriminant responding towards a contingent vs. non-contingent partner emerges.

The gradually emerging sensitivity to social contingency observed also implies that in the pigeon, meaningful social contingencies may have a fairly ‘loose’, imprecise temporal structure. In other words, the temporal window in which a social response successfully sustains the stability of the interaction may be relatively large. Pigeon courtship is far from being a ritualized duet; rather, the coherent structure of the courtship interaction seems to show substantial variation
across pairs, within pairs and across time. Social responsiveness may be especially critical for this ‘loose’ form of social coherence since behavioural patterns cannot be described by a predictable ritualized behavioural template, or choreography, as is the case for vocal duetting (Malacarne et al. 1991).

Given the highly controlled method of manipulating social contingency employed in the present study, thereby creating a good ‘illusion’ of social coherence, it is perhaps not surprising that the observed experimental effects are very subtle. What mechanisms might underlie these effects?

3.4.3.1 Possible mechanisms

Historically, the most common logic used to explain evidence for a subject’s behavioural sensitivity to social contingency has been that, since the experimental stimuli vary only by the degree of contingent responsiveness present in the partner’s behaviour, the subject must be cognizant about their partner’s behaviour as being in response to their own actions (Friedman 1977; Murray and Trevarthen 1985; Hains and Muir 1996; Nadel et al. 1999; Trainor and Basolo 2000; Ord and Evans 2002; Miller et al. 2009). This notion has recently been questioned and it has been proven that social response detection is not the sole mechanism that might underlie interactive behaviour (see p.37) (Di Paolo et al. 2008; Auvray et al. 2009; Froese and Di Paolo 2010). It turns out that social dynamics can be sensitive to social contingency due to their reliance on perceptual crossing dynamics, where two perceptual behaviours of the same nature simultaneously ‘cross’ (e.g. eye contact). Perceptual crossing elicits a mutually congruent response that increases the likelihood that the perceptual crossing event will re-occur, thereby creating a dynamic that perpetuates itself as well as the behaviour of the individuals making up the system (Di Paolo et al. 2008). Thus, there are, not just one, but two existing frameworks to help explain the present findings: partner response detection and perceptual crossing dynamics.
Partner response detection is a mechanism occurring at the ‘individual’ level within the bird’s psychology and perceptual crossing dynamics describe a process influencing behaviour by affecting the dynamical ‘system’ of social interaction. The findings will be discussed in terms of each interpretive framework separately; however, these explanations are not mutually exclusive. Rather, social response detection and social dynamics represent two potentially inter-dependent processes that can influence behaviour at different levels of the social interaction (De Jaegher and Froese 2009).

3.4.3.2 Response detection

The explanation that pigeons are detecting their partner’s responses essentially implies that pigeons detect and evaluate, on some level, when their partner’s social displays are related to their own social behaviour.

The data provide some support for this hypothesis. The slight decrease in courtship intensity towards non-responsive social partners might indicate what is commonly referred to as learned helplessness, where organisms appear to learn that their actions are inconsequential (Maier and Seligman 1976; Alloy 1982; Tennen et al. 1982). For instance, human infants become fussy when communicating with an unresponsive caregiver. This has been interpreted as evidence that the infant’s expectation for their caregiver’s responsiveness has been violated; in learning that they are helpless, the infants start to cry (Murray and Trevarthen 1985; Nadel et al. 1999). The classic example for learned helplessness in the field of animal learning is Maier and Seligman's (1967) experiment, where two groups of dogs were given electric shocks. One group could end the shocks by pressing a lever. Another group of dogs were wired in parallel with the first group and could not control the electric shocks. To a dog in the latter group, the shocks were apparently inescapable and uncontrollable. The dogs that could control the shocks quickly
recovered from the experience, whereas the other group learned to be helpless, and exhibited symptoms similar to chronic clinical depression in humans (Alloy 1982).

It is possible that the decrease in pigeon circle walking behaviour in Playback conditions lacking social contingency reflect a type of learned helplessness. Just as animals may learn the relationships between their actions and a reward in operant conditioning paradigms, social behaviour might be navigated by learning the causal connections between their own behaviour and subsequent social outcomes. A pigeon in the Playback condition may have learned the inefficacy of their social behaviour and responded by decreasing their inconsequential displays. According to Maier and Seligman (1976), an animal must possess an expectation for responsivess and then detect non-responsiveness before the animal can form the expectation of future non-responsiveness, which then can lead to a change in behaviour. In the pigeons, the cognitive processes leading from a detection of non-responsiveness to an expectation of future non-responsiveness could be influenced by prior (previously learned) expectations about social responses that regularly occur in circle walking interactions.

There are a number of possible cognitive mechanisms by which sensitivity to a partner’s responsiveness could occur. First, pigeons may access response information by directly evaluating social contingency. Social contingency detection requires pigeons to learn action-outcome expectancies from the conditional probabilities between signals and responses, and use their learned expectations to help identify which subsequent partner behaviours are responses and which ones are not (Tarabulsy et al. 1996). Another possibility is the use of heuristics to infer social contingency rather than calculating it directly (Watson 1985; Gergely and Watson 1999; Watson 2001). In particular, the timing and spatial directionality of the social response are powerful cues to the signaler that a partner’s display is in response to their own (Watson 1985). Another possible heuristic for communicating responsiveness would be to match some aspect of the circle walking dynamics to the initiating display, like intensity, frequency or form (Watson
Matching signals is thought to function as a cue for social responsiveness in species across several taxa (Suguira 1998; Beecher et al. 2000; Janik 2000; Sharpley et al. 2001; Lakin et al. 2003; Miles et al. 2009) and could occur between a variety of local or global dynamic features of pigeon display behaviour, like signal intensity, type, frequency or style.

Instead of rigidly using specific heuristics, it is possible that the pigeon’s sensitivity to social contingency is indicative of a more complex understanding of its own species social dynamics. The mechanisms subserving this social ‘understanding’ could be conceptualized as those recruiting all available social statistics and heuristics to generate a sophisticated awareness of social dynamics (Gergely and Watson 1999). The available cues are manifold, and include social contingency, response timing, spacing, relative signal content, relative signal intensity, as well as how the meaning of these cues vary depending on the specific social context of the interaction, taking into consideration factors like rank relationships, social status and social bonds. The combination of cues used would likely vary for each specific type of signal-response relation and depend on the unique meaning of natural variation in its structure. For instance, if a male pigeon circle walks and a nearby female starts to circle walk as well, a temporal-spatial contiguity between the two circle walking displays may be perceived as courtship responsiveness more so if the female is alone and appearing single than if she is standing near her own mate.

Further experiments are required to resolve whether or not pigeons can detect partner responses and what mechanisms might underlie this sensitivity. Also, the individualistic explanations for social contingency sensitivity in pigeon behaviour must be properly balanced with an exploration of alternative hypotheses that focus on the dynamics of the interactive process (Di Paolo et al. 2008; Auvray et al. 2009; Froese et al. 2010).

3.4.3.3 Perceptual crossing
An alternative framework that may explain the pigeon’s behavioural sensitivity to social contingency describes interactive processes on a system dynamics level rather than by mechanisms present in the psychology of the animal, like response detection. This ‘dynamical’ account purports that the coherence of the pigeon’s courtship interaction increases when two perceptual events of the same nature simultaneously ‘cross’. Such an event can simultaneously trigger a mutually congruent behavioural response in both pair members, creating a dynamic that increases the probability that the perceptual crossing will re-occur again and again, thereby promoting the ‘ongoingness’ of the social dynamic (Di Paolo et al. 2008; Froese and Di Paolo 2008; 2010; Auvray et al. 2009). In the context of pigeon interaction, a perceptual crossing event that acts to sustain circle walking behaviour would entail the simultaneous perception of, and reaction to, some critical aspect of courtship behaviour.

There are a number of pigeon behaviours which could be involved in perceptual crossing, including eye contact, or simultaneous action involving head-bobbing, bowing, a single circle or the circle walking bout. If the simultaneous performance of, perception of and reaction to any of these events increases the probability that a perceptual crossing dynamic will repeat recursively, this could explain the sensitivity of the pigeon’s behaviour to social contingency manipulations in courtship. The decrease in behaviour observed in Playback conditions would occur because, in the absence of reciprocal contingencies, the perceptual crossing event becomes ‘uncrossed’, resulting in perceptual and behavioural interactions that do not perpetuate the social dynamic, nor the circle walking behaviour making up that dynamic.

3.4.3.4 Conclusion

This experiment shows that pigeon courtship can be described as an interactive process that requires intact mutual responsiveness between partners to maximize each pigeon’s circle walking behaviour. However, the data cannot determine the exact mechanisms responsible for the
effects of social contingency on behaviour. There are several potential explanations for the decrease in behaviour that occurred when social contingency was disrupted in the Playback condition. These range from the several ways a pigeon might learn about their partner’s non-responsiveness, to the disruption of any number of possible perceptual crossing dynamics that normally potentiate circle walking behaviour in courtship. Together these alternative, but not mutually exclusive, explanations imply a potentially complicated picture of the mechanisms underlying the pigeon’s interactive social behaviour. To unravel these mechanisms in the pigeon, a research protocol aimed at differentiating the psychological response detection mechanisms from dynamical systems perceptual crossing mechanisms is the next logical step. The following experiments present one approach to this problem. We manipulate the spatial structure (Experiment 3) and temporal structure (Experiment 4) between two interacting pigeons and observe the effects of these distortions on behaviour. Although this approach alone did not result in any solid conclusions about the mechanisms underlying interactive behaviour in the pigeon, we hope to at least gain a better idea about which social contingencies might be behaviourally relevant in courtship. By distorting the timing and spacing between courting pigeons we can narrow down the possible response detection or perceptual crossing mechanisms that might be responsible for interactive behaviour in this species.

3.5 Experiment 3: Sensitivity to the facing direction of a social partner

The finding that the pigeon’s courtship behaviour was interactive – pigeons reduced their courtship intensity when the social contingency between their own behaviour and that of a social partner was disrupted (Experiment 2) - might be explained by at least two spatially sensitive processes. First, if pigeons possess capacities to understand social responsiveness, the facing direction of a partner’s signaling behaviour might be a particularly informative and accessible cue for recognizing a partner’s responses. Second, the facing direction of a partner’s display might be
important in perceptual crossing, the event that the perceptual activities of two communicating animals interact in ways that are important maintaining the social dynamics of courtship. Of the perceptual crossing events that may be responsible for interactive circle walking behaviour in pigeons, like eye contact or simultaneous head bobbing, bowing, circling or circle walking, some of them would require pigeons to face each during courtship in order for the bird’s perceptions to ‘cross’. The influence of a partner’s facing direction on the subject’s courtship behavior can therefore help narrow down which social contingencies might be relevant during courtship interactions.

Previous studies testing the pigeon’s sensitivity to the facing direction of a partner’s display have yielded mixed results (Friedman 1977; Troje et al. unpublished). Troje (unpublished data) investigated male pigeons’ courtship behaviour towards an animated ‘virtual’ female pigeon programmed to display either facing towards the subject or in a direction 90° away from the subject. The courtship behaviour of the virtual female was driven by the motion dynamics of a live courting female pigeon which was collected with motion-capture technology. The male subjects increased their courtship intensity when they viewed the virtual female courting in a direction 90° away from them compared to viewing the female courting directly towards them. Troje suggests that, in natural conditions, a female facing away from a male might indicate the presence of a sexual competitor and that males may adaptively react by increasing their courtship intensity to attract the female’s attention away from the other male. While Troje’s results suggest that male pigeons are sensitive to the female’s facing direction, it cannot be ruled out that the results reflect an artifact of using an unnatural virtual female as a social partner.

Friedman (1977) showed that a female ring dove viewing a male across clear glass, who could also see and direct his courtship towards her, experienced greater ovarian development than a second female who viewed the same male across one-way glass, who directed his courtship 90° away from her (towards the first female). Since the two females experienced differences in visual
stimulation that included both a spatial factor as well as differences in social contingency, the effects of partner facing direction and the effects of contingency were confounded. Friedman argued that the male’s behaviour did not appear spatially directed except for the first day, during which males were courting. He argued that since courtship is highly aggressive, it may actually delay female reproductive development, and therefore this first day of courtship likely had little impact on the observed growth of the female’s reproductive physiology. After the first day the frequency of courtship dropped and the males began spending their time nest soliciting, which is thought to be an important stimulus for female reproductive growth. Since the males did not appear to be facing towards either female during the time they were nest soliciting the author suggested that the female’s sensitivity to male responsiveness was the most likely factor affecting female ovarian growth and the spatial directionality of the male’s social behaviour was not (Friedman 1977).

In this experiment, male and female pigeons are tested for behavioural sensitivity to the facing direction of their partners’ display behaviour. Partner facing direction is varied by manipulating the camera angle filming the subject’s partner, so that the partner appears to direct its courtship 90° away from the subject. In addition, we crossed the experimental factor of facing direction with the manipulation of social contingency, using Live and Playback conditions (see Experiment 1). This design can assess the influence of facing direction and social contingency, both separately and in combination, on pigeon courtship behaviour.

It is predicted that this experiment will replicate the finding that pigeons behave interactively in courtship (Experiment 2). Manipulating the facing direction of the partner’s display will help to reveal to what extent the pigeon’s interactive behaviour depends on the directionality of the partner’s contingent social responses. Furthermore, sensitivity to facing direction can give clues to the type of social contingency, be it signal response contingencies or perceptual crossing events that pigeons are sensitive to. For instance, pigeons may use spatial
contiguity between themselves and their partner’s display directionality as a cue to infer their partner’s responsiveness. Alternatively, a perceptual crossing event that is spatially precise, like making eye contact or simultaneously perceiving one another’s mutually directed actions, like bowing or charging, would be ‘uncrossed’ in conditions manipulating the facing direction of the partner’s display. However, if pigeon courtship is not sensitive to their partner’s facing direction this would indicate that the social contingencies that are relevant to interactive behaviour are not spatially precise. Spatially imprecise signal-response contingencies and perceptual crossing events, like responding to circle walking with circle walking, or, circle walking simultaneously, would not necessarily be disrupted by manipulating the partner’s facing direction. In this way the results of this study will help to formulate hypotheses about the quality and type of social contingencies that are relevant to pigeons in courtship.

3.5.1 Methods

3.5.1.1 Subjects and stimuli

For Experiment 3, six male and six female pigeons were used. As in Experiment 2, the birds were paired in every possible opposite sex pair combination to yield 36 opposite sex pairs of birds.

The four conditions mixed two experimental factors with two levels each: the partner’s facing direction was either towards the subject (0°) or directed away from the subject (90°), and social contingency was either intact (Live) or not (Playback). With these two factors, four conditions were created: Live-0°, Live-90°, Playback-0° and Playback-90°.

The 90° spatial offset manipulation was achieved by placing a second tripod for filming the partner at a camera angle located 90° away from the camera inside the teleprompter apparatus. The placing of the tripod - to the left or the right of the stimulus pigeon was counter-balanced across conditions. Since the 90° offset condition involved removing the camera from the
teleprompter apparatus, a pane of glass was fitted on a 45° angle in front of the camera lens to match the filming quality obtained from the camera within the teleprompter. Black chloroplast plastic board was placed on the top and the sides of this camera setup to prevent glare on the glass from the room lights.

3.5.1.2 Experimental design

Each trial contained six minutes of social interaction. As opposed to the three, 2 minute segments in Experiment 2, there were no breaks within a single trial. We changed this detail after speculating that birds may become more sensitive to social contingency later in the trial when circle walking is less stereotyped and more unpredictable, and therefore social contingencies may become more important in sustaining interaction (Figure 7).

All 36 pairs underwent all four conditions twice, so that the female and the male each acted as the subject once for all four conditions. The yielded a total of 288 experimental trials.

3.5.1.3 Analysis

Three 3-way repeated measures ANOVAs [2 (sex) x 2 (facing direction) x 2 (contingency)] were performed to evaluate these experimental effects on courtship behaviour. The three ANOVAs correspond to the subject’s total circle walking duration, average bout duration and number of circle walking bouts. Bird sex was treated as a between subjects factor while facing direction and contingency were treated as within subject factors. The random variable was the subject (N= 12). To further investigate the main effects of the experimental conditions on circle walking behaviour, three pairwise t-tests were used to compare the Live-90°, Playback-0° and Playback-90° with the Live-0° condition. A Bonferroni corrected alpha level of 0.0167 was used to evaluate significance. Experimental effects showing a p < .05 were identified as being marginally significant.
3.5.2 Results

In Experiment 3, there was no significant effect of facing direction on any measure of subject circle walking duration. The study did, however, replicate the effect of social contingency on total circle walking duration, $F(1, 10) = 16.79, p = .002$, and on average bout duration, $F(1, 10) = 15.46, p = .009$. The number of bouts also differed significantly across contingency conditions, $F(1, 10) = 11.05, p = .008$.

For total bout duration, pairwise t-tests show a significant difference between Live-0° and Playback-90° conditions, $t(11) = 3.59, p = .004$. For average bout duration, the t-tests reveal a marginally significant difference between Live-0° and Playback-0°, $t(11) = 2.23, p = .047$, and a significant difference between Live-0° and Playback-90°, $t(11) = 3.81, p = .003$. For number of bouts, there was a marginally significant difference between Live-0° and Playback-0°, $t(11) = -2.31, p = .041$ and a significant difference between Live-0° and Playback-90°, $t(11) = -3.01, p = .014$. The results are shown in Figure 8.

Sex differences in circle walking behavior were similar to those observed in Experiment 2 (Figure 6). Males circle walked for longer average bout durations, $F(1, 10) = 12.83, p = .005$, and exhibited a fewer number of bouts, $F(1, 10) = 21.03, p = .001$, than females.
The results show that pigeon circle walking is sensitive to social contingency but not to the cues present in the partner’s facing direction. These findings suggest that a pigeon’s interactive circle walking behavior does not depend on social contingencies that require partners to face each other directly. The black asterisk (*) indicates significant differences (p < 0.0167) and the gray asterisk (**) indicates a marginally significant differences (p < 0.05) between the marked condition and the L-0° condition. L = Live and P = Playback.

3.5.3 Discussion

Experiment 3 showed that pigeon circle walking duration did not significantly differ when a partner’s facing direction was oriented 90° away from the subject. There are three possible explanations for this finding: 1) that pigeon circle walking does not contain directionality cues, 2) that pigeons lack perceptual or behavioural sensitivity to a partner’s facing direction, i.e. orientation cues lack behavioural relevance and 3) that our experimental assay was insensitive to the effects of partner facing direction on courtship behaviour resulting in a type II error.

3.5.3.1 Directionality cues in courtship

With regard to the existence of cues to a pigeon’s facing direction in courtship, the personal observations made during the course of this study are in agreement with Friedman’s (1977) notes about ring doves, that the pigeon courtship display does contain several conspicuous
directionality cues. For instance, when a pigeon is standing still and head-nodding (in females) or bow-cooing (in males) they typically stand as close as possible to the image of their partner on the teleprompter and face the partner in a clearly directional fashion. Additionally, the dynamics of the circle walk appear spatially oriented towards the social partner; the segments of the circle that move towards the partner typically appear to include more charge, tail drag and bowing motions than the segments of the trajectory moving away from the partner. Thus, while the circle walk lacks directionality to some degree because of its circular trajectory, information about facing direction is clearly available.

3.5.3.2 Visual sensitivity to directionality cues

If a human observer can readily perceive the directionality cues in pigeon courtship then these cues are likely to be available to the pigeon as well. Pigeons are popular laboratory animals not primarily for their social behaviour but for their impressive visual discrimination and object categorization abilities. Among these abilities, the pigeon has been shown to be capable of categorizing visual stimuli based on dynamic features, such as whether an object passes through or over another object (Cook et al. 2001; Cook and Roberts 2007). Considering the pigeon’s adept visual discrimination abilities, it is unlikely that a pigeon is incapable of discriminating between a partner displaying away from them and a partner displaying towards them.

3.5.3.3 Behavioural sensitivity to directionality

It is possible that the dynamic properties of courtship display that influence circle walking behaviour do not vary appreciably with the display’s orientation. This might reflect natural selection for sexual display features that effectively influence multiple recipients located at various possible viewing angles. A signal design that could stimulate multiple receivers simultaneously would be adaptive in the context of advertising fitness, since this would allow the signaler to influence many potential mates and competitors at once. From the perspective of the
signal receiver, it is possible that the courtship display’s directionality is not relevant to the circle walking response. Whether a conspecific is courting towards or away from the receiver, the adaptive circle walking response may remain the same, especially under conditions promoting intense motivation for courtship such as the socially isolated living conditions that the subjects experienced in the present study. Behavioural insensitivity to signal orientation has also been observed in the Jacky Dragon lizard’s (*Amphibolurus muricatus*) response to conspecific visual displays of aggression (Peters et al. 2007). The multidirectional design of circle walking as well as the robustness of response behaviour across variations in the display’s facing direction may reflect a hallmark of visual signals adapted for multirecipient broadcast in colony settings.

The discrepancy between the present findings and those of Troje et al. (unpublished), might be explained by the possibility that the male subjects in Troje’s study perceived the virtual pigeon not as a female pigeon, but perhaps as a male pigeon or another dove species entirely. In other words, Troje’s finding that males increased their behaviour in response to conspecifics displaying away from them might reflect the male’s sensitivity to the directionality of visual display in interactions with another type of social partner. Unfortunately, the present study did not test the effect of display orientation on circle walking behaviour in any social context other than courtship and therefore this study is unable to confirm this suggestion.

Another difference between Troje’s study and the present one is the behavioural measure used. In Troje’s study human raters evaluated their overall impression of the male’s circle walking intensity on a scale from 1 to 100. This measure is likely to be much more sensitive to the differences in various signaling components of the circle walk, like bowing cooing and tail dragging as well as their relative intensity, frequency and duration. As we will discuss below, the discrete signaling behaviour within pigeon courtship may be more sensitive to a partner’s facing direction than circle walking is.
3.5.3.4 Type II error

The findings could be the result of a Type II error, attributable to the insensitivity of the behavioural measure used. It is important to note that for the response measure of circle walking duration the sample size was sufficient to detect an effect of social contingency. Therefore any putative effect of partner display orientation on circle walking duration must be small, relative to that of social contingency.

A likely possibility is that the various components collectively defining courtship intensity (e.g. circle walking duration, number of bows, number of coos etc.) may vary independently from one another and exhibit differential sensitivity to a social partner’s facing direction and a social partner’s contingency. While circle walking duration may be sensitive to social contingency, this particular behaviour may be insensitive to a partner’s facing direction. This interpretation is concurrent with Galoch and Bischof’s (2007) findings in a study investigating zebra finches. His experiment showed that the effect of a female’s facing direction on male behaviour differed depending on the behavioural measure used to assess male behaviours. The female zebra finches were filmed either alone, or with another zebra finch present in the cage adjacent to them (outside the frame of the video recording and 90° away from the camera’s viewpoint). Galoch and Bischof found that the male’s courtship song and his proximity to the monitor did not significantly depend on the female’s facing direction but the males’ beak wiping behavior and “Tit” and “Tet” calls did (Galoch and Bischof 2007).

Taken together - the negative finding of facing direction on circle walking behaviour, the evidence that a holistic assessment of pigeon ‘courtship intensity’ does show sensitivity to facing direction (Troje et al. unpublished data) and the findings in zebra finches showing that different behavioural measures can be differentially sensitive to a partner’s facing direction (Galoch and Bischof 2007) - these studies lead to one suggestion in particular. Perhaps as a general rule, behaviours described as ‘continuous’ display, like the courtship song of the zebra finch or the
circle walking display of the pigeon do not show sensitivity to facing direction because they do not serve an attention-grabbing function. The duration of circle walking might instead serve to convey fitness information about physical endurance (Burley 1981). On the other hand, discrete, abrupt behaviours like the zebra finches beak wipes and ‘Tit’ and ‘Tet’ calls and the pigeon’s vocal coos, vigorous bowing and sharp charging movements may better serve the function of grabbing a conspecific’s attention. In Troje’s study, the pigeons’ discrete courtship bows, coos, charges and tail drags as well as their relative intensity would have been reflected in the experimenter’s evaluation of the display’s ‘overall intensity’. It is logical that behaviours with a sharp temporal curve would have evolved to trigger the visual grasp reflex and serve to attract conspecifics’ attention (Fleishman 1988). By this reasoning, circle walking duration should not be modulated by the facing direction of a partner’s display because such a change would have little influence on the partner’s spatial attention. Instead subjects that are interacting with a partner that is facing away from them could draw their partner’s attention by increasing the amplitude and frequency of bowing, cooing, tail dragging and charging behaviour. Thus, the pigeons may well distinguish spatial directionality, but they court with the same circle walking intensity nonetheless.

3.5.3.5 Implications for understanding interactive behaviour

The primary goal of this experiment was not simply to understand the pigeon’s sensitivity to directionality cues in a partner’s courtship display, although this is an interesting question, but to ascertain if the pigeon’s sensitivity to social contingency relies, in part, on spatial cues. Specifically, the investigation aimed to test the predictions of the two mechanisms previously discussed for explaining interactive behaviour in the pigeon, partner response detection and sensitivity to the dynamics of perceptual crossing.
3.5.3.6 Response detection

If the pigeon has a complex understanding of partner responsiveness, one would expect this understanding to capitalize on the rich information contained in the facing direction of a social partner’s signals. Taken alone, the findings of this study appear to suggest that pigeons do not have a complex causal understanding of their social interactions. However, after considering that other behaviours within courtship may be modified in response to a partner’s facing direction, the hypothesis that pigeons do use spatial cues to infer partner responsiveness, and that this process might be measured better with a different behavioural assay, cannot be discarded. The fact that the pigeon did not adjust its circle walking behaviour according to facing direction implies that the interactive circle walking behaviour observed does not rely on a mechanism for sensing partner responsiveness that uses spatial cues. It is possible that the pigeon’s sense of social responsiveness is so flexible that even when a partner appears to be facing away the subject can still recognize the social influence they have on their partner’s behaviour. This might occur if the cues that are relevant to inferring responsiveness are present in non-directional behaviour, like the timing of the contingencies between circle walking bouts. Since circle walking may be used for signaling towards multiple recipients at once, if a subject is circle walking and the partner starts circle walking shortly after, the facing direction of the partner’s display may not be required, or useful, for identifying that display as a social response. Instead temporal relations between circle walking bouts may be more important and this possibility will be tested in Experiment 4.

3.5.3.7 Perceptual crossing

We can begin to shape hypotheses about which social contingencies in courtship might be classified as perceptual crossing events in circle walking interactions, and which could not. The findings rule out any perceptual crossing events that can be described by precise spatial
directionality, like eye contact or the mutual facing direction between either dynamic or stationary courtship behaviours. What remains are perceptual relations that do not depend on mutual facing behavior. Remaining behavioural candidates for perceptual crossing dynamics might be simultaneous bowing, congruent dynamics between circling trajectories and simultaneously performed circle walking bouts. Of these, the circle walking bout would likely be the least spatially sensitive ‘crossing’ behaviour, but given the pigeon’s wide visual field, discrete behaviours like bowing and the circle’s trajectory should not be ruled out either. To use the circle walking bout as an example, if two pigeons are circle walking at the same time their simultaneous perception of and reaction to this event might produce courtship dynamics that depend on the simultaneous ‘crossing’ of circle walking and at the same time make it more likely for this ‘circle walking crossing’ event to re-occur (as described by Froese and DiPaolo 2008). If this is the case, interactive circle walking behaviour should be sensitive to time delays that reflect the average length of the relevant perceptual crossing event. This possibility will be tested in Experiment 4.

3.5.3.8 Conclusion

On the whole, the results imply that circle walking duration may not function to elicit the attentional reflexes of a conspecific facing away. A different function that circle walking duration more likely serves is that of communicating information about physical endurance. One can therefore begin to paint a picture of the pigeon’s courtship display and the function of its components. Circle walking is suited to be assessed by multiple recipients appraising the signaler’s endurance and fitness. On the other hand, the discrete elements embedded within circle walking, such as bowing, tail-dragging, charging, nodding etc., likely function primarily to grab the attention of conspecifics or to exert other influences on a partner’s behaviour based on the specific demands of the situation.
With respect to the pigeon’s interactive behaviour, the relevant social contingencies do not appear to be characterized by a precise spatial profile. Instead the relevant social contingencies must lie between behaviours that lack precise spatial orientation. One possibility is that the timing, not the spacing, between potentially relevant behaviours like bows, circle trajectories or circle walking bouts is instrumental in interactive behaviour. More specifically, either the pigeon’s social response detection abilities and/or the perceptual crossing dynamics of courtship may depend on the temporal relations between behaviours to remain intact.

3.6 Experiment 4: Sensitivity to timing and social context

The present experiment aims to further explore the mechanisms underlying the pigeon’s interactive courtship behaviour by: 1) manipulating the timing of social contingencies, and 2) testing the social contingency sensitivity of circle walking behaviour across two different social contexts, courtship and competitive rivalry interactions.

The time delays selected for this experiment, 1s, 3s and 9s, can help refine predictions about the potential mechanisms underlying interactive behaviour in pigeons. Under the response detection framework, the timing between behaviours may be used as a heuristic for identifying a partner’s responses. Watson (1966) has suggested that 3s characterizes the timeframe that is used by human infants to make inferences about social responsiveness. Since the 3s window defines the typical timeframe in which social responses typically occur in birds as well as in humans (Todt and Fiebelkorn 1980; Odom and McConnell 1985) it may represent an accurate heuristic for identifying social responses across species. One might expect evolutionary convergence in the temporal heuristics used for response detection, since many fundamental constraints on response timing are consistent across species. One prediction of the response detection framework therefore might be that 3s delays will mark a boundary for the influence of social contingency manipulations on pigeon courtship behaviour, as it does for human infants. Although, it is not
certain that this purported 3s boundary for response detection applies consistently across different types of social contingencies or across different species, so of course, we must be cautious in drawing conclusions about response detection in pigeons from the logic constructed in work on human infants.

Under the perceptual crossing framework, a time delay condition that exceeds the length of any relevant perceptual crossing events that act to sustain the social dynamic is predicted to impair the stability of the interaction and thereby depreciate the intensity of each subject’s circle walking behaviour, as was observed in the Playback condition of Experiment 2. To target specific behavioural candidates for perceptual crossing the three time delays chosen to each approximate the durations of different pigeon behaviours, bowing (1s), a single circle (3s) and a circle walking bout (9s).

In pigeons, the mechanisms underlying interactive behaviour will be linked to and shaped by the function of this behaviour (if any). While both opposite sex and same sex social partners elicit circle walking behaviour in the pigeon, the distinction between intra-sexual competition and inter-sexual mate choice in shaping social display is well established in sexual selection theory (Andersson and Iwasa 1996). Given the diverging evolutionary selection pressures on behaviour across same sex and opposite sex social encounters, the prediction is that the influence of social contingency on behaviour will differ across these two social contexts.

3.6.1 Methods

3.6.1.1 Stimuli

This experiment contains five conditions. The Live condition is a real-time interaction where both subjects can act contingently towards each other. There are three time delay conditions to assess the sensitivity of behaviour to the timing of social contingency; the delays used are 1s, 3s and 9s. The Playback condition is the presentation of video playback of the
subject’s social partner that was previously recorded during that pair’s Live condition, which effectively creates a non-contingent social stimulus. We test all five conditions in two different social contexts: opposite-sex (courtship) interactions and same-sex (rivalry) interactions.

3.6.1.2 Experimental design

We ran this experiment twice, first with 12 birds (Block 1) and then with 6 more subjects (Block 2). For courtship interactions, all possible combinations of male and female birds were used, yielding 36 pairs in Block 1 and 9 pairs in Block 2. For rivalry interactions, all possible combinations of two male birds or two female birds yielded 15 male-male and 15 female-female pairs in Block 1 (30 pairs in total), and 3 male-male and 3 female-female pairs in Block 2 (6 pairs in total). In Block 1, each dyad from all courtship and rivalry interactions experienced all five experimental conditions, yielding 180 courtship and 150 rivalry trials. In Block 2 each pair underwent each condition twice. Since there were fewer subjects in Block 2 repeating each condition twice for each pair ensured that in Block 2 each individual underwent the same number of trials for each condition as in Block 1. This yielded 90 courtship and 30 rivalry interactions in Block 2. In combining Block 1 and Block 2, there were 270 courtship and 180 rivalry interactions in total. Experimental trials were 6 minutes in duration.

The time delay and video playback conditions were always implemented as unidirectional manipulations. However, in order to collect as much data as possible, both birds in each trial are conceptualized to be equal subjects. In doing so, the data available for analysis was doubled, resulting in a total of 540 courtship and 360 rivalry subject videos for analysis. The justification for this is that in a closed-loop communication circuit, a unidirectional manipulation is assumed to always affect both subjects bi-directionally, in an equivalent fashion. For example, for a time delay travelling from the female camera to the male’s stimulus display, the male bird will experience social responses that are delayed in time and the female will experience the same
social delay due to the male’s delayed response behaviour. The same reasoning can be made for the Playback condition. In the Playback condition, pigeon A sees a video playback of pigeon B and pigeon B sees a real-time video of pigeon A (who is interacting with the video playback of pigeon B). Neither subject can influence the behaviour of its partner, although the partner’s behaviour is otherwise either identical or motivationally equivalent to the control condition. Thus, in every trial both pigeons are considered to be a ‘subject’ as well as a ‘partner’. The directionality of temporal delays and Playback manipulations were counterbalanced across all subjects.

3.6.1.3 Analysis

The measures of total circle walking duration, average bout duration and number of circle walking bouts, obtained with automatic motion energy coding (Experiment 1), were used to analyze subjects’ circle walking behaviour. After verifying that there were no differences in the data collected in Block 1 and Block 2 we combined all data together for analysis. We conducted three 3-way [2 (sex) x 2 (social context) x 5 (contingency)] repeated measures ANOVAs corresponding to each of the three measures of circle walking behaviour. Sex is treated as a between-subjects factor and social context and social contingency are treated as within-subject factors. The bird was treated as the random variable (N=18). The main effects of all ANOVAs were evaluated using an alpha level of .05. In finding an interaction between social context and social contingency we performed another set of three 2-way ANOVAs [2 (sex) x 5 (contingency)] separately for each social context. In finding an interaction between contingency and sex in the social context of courtship, two 1-way ANOVAs [2 (sex) x 5 (contingency)] were used to assess the effects of contingency separately in each sex. An alpha value of 0.05 was used to assess significance in the ANOVAs. In finding a p < 0.06, the effect was identified as being marginally significant. For all ANOVAs showing a significant effect of social contingency on behaviour, 4
pairwise t-tests were used to compare the circle walking values in each time delay condition (1s, 3s, 9s delays) as well as the Playback condition with those measures in the Live condition. A Bonferroni corrected alpha of .0125 was used to assess significance. T-tests producing p<.05 were taken as marginally significant effects.

3.6.2 Results

3.6.2.1 Social context

Total circle walking duration was significantly affected by social context, with more activity during courtship than in rivalry interactions, $F(1, 16) = 53.83, p < .001$. This can be explained by the effect of social context on average bout durations, $F(1, 16) = 10.21, p = .006$. These effects can be observed in Figure 9.

3.6.2.2 Social contingency

There was a main effect of social contingency on total circle walking duration $F(4, 64) = 5.46, p = .003$. This effect of contingency on total circle walking duration depended significantly on the social context, $F(4, 64) = 3.53, p = .011$ (Figure 9), therefore the data for each social context was analyzed separately.

The follow up ANOVAs revealed a significant effect of social contingency on total circle walking duration in opposite-sex interactions, $F(4, 64) = 7.75, p < .001$, and no significant effect in same sex interactions. The t-tests revealed that total circle walking duration significantly decreased between the Live and 9s conditions, $t(17) = 4.29, p < .001$, as well as between the Live and Playback conditions, $t(17) = 4.14, p = .001$.

The analysis revealed a main effect of social contingency, $F(4, 64) = 6.55, p < .001$, and a significant interaction between sex, social context and contingency, $F(4, 64) = 3.36, p = .036$, on average bout duration. Follow up ANOVAs revealed a significant effect of social contingency on male average bout duration in courtship interactions, $F(4, 32) = 5.01, p = 0.003$, but no effect
in females or in any rivalry interactions. Post hoc analysis on the male courtship data revealed a marginally significant increase between Live and 3s, $t(8) = -2.51, p = .036$, in male average bout duration (Figure 10).

There was a marginally significant interaction between sex, social context and contingency, $F(4, 64) = 2.41, p = .058$, on the number of circle walking bouts. Follow up ANOVAs revealed a marginally significant effect of social contingency on female bout frequency, $F(4, 32) = 2.85, p = 0.055$, in courtship only but no effects in males. T-tests revealed a marginally significant decrease between Live and 9s, $t(8) = 2.53, p = .035$, in number of female bouts (Figure 10).

3.6.2.3 Sex

The effects of pigeon sex on circle walking behaviour were similar, but slightly different than those found in Experiment 2. Unlike in Experiment 2, males and females significantly differed in total circle walking duration, $F(1, 16) = 11.42, p = .004$. Also, the present results show no significant effect of sex on number of bouts. Males did however show significantly longer average bout duration than females, $F(1, 16) = 61.13, p < .001$, as they did in Experiment 2. These results are shown in Figure 11.
Figure 9. The effect of contingency on circle walking behaviour depends on the social context

Pigeon circle walking behavior is interactive in courtship but not in competitive interactions between rivals. The total circle walking duration, average bout duration and total number of bouts are shown for each social contingency condition across opposite sex (courtship) and same sex (rivalry) interactions. In courtship only, the 9s delay condition and the Playback condition produced significant effects on circle walking behavior. The black asterisk (*) denotes a Bonferroni corrected significance level (p < 0.0125).
Male pigeons, but not female pigeons, show a marginally significant increase in their average bout duration in the 3s delay condition. In female pigeons the number of circle walking bouts is sensitive to social contingency and shows a decrease in the 9s delay condition. The gray asterisk (*) denotes a marginally significant difference (p < 0.05) between the marked condition and the Live condition.

Figure 10. Interactions between sex and social contingency on circle walking behaviour
Figure 11. Sex differences in circle walking behaviour II

Male and female pigeons each have distinct patterns of circle walking behavior. The pattern observed in the present experiment is slightly different from that observed in Experiment 2 (see Figure 6). In the present experiment, males exhibit greater total circle walking duration and greater average bout duration than females. Significant differences between male and female circle walking are indicated by the asterisk (*) over the female data point, $p < 0.05$.

3.6.3 Discussion

This experiment tested a simple but meaningful parameter characterizing the social contingency between two pigeons’ social display behaviours in courtship and rivalry interactions. The results provide evidence that inter-signal timing is instrumental in shaping interactive circle walking behaviour. Furthermore, the effects of social contingency manipulations on circle walking behaviour appear to be unique to courtship interaction. The specific mechanisms underlying the sensitivity of circle walking behaviour to social contingency and its timing are still not clear from these data alone. The pattern of results across time delay conditions implies that interactive circle walking behaviour relies on mechanisms with a temporal boundary lying between 3 and 9s. For the male pigeon, the finding that circle walking behaviour marginally increases when social contingencies were delayed by 3s is surprising. Since social interactivity is typically conceptualized as constituting a set of mechanisms for potentiating and sustaining social interaction, disrupting social coherence was expected to produce a decrease in circle walking behaviour, rather than the increase observed in males.
Here, the mechanisms that might underlie the observed effects of social contingency on circle walking are discussed. We address the question of whether interactive behaviour plays a special role in courtship interaction last.

3.6.3.1 Response detection

The findings do not wholly support, nor do they refute the idea that interactive behaviour in pigeons reflects their ability for response detection. There are two ways in which temporal delays might disrupt social response detection. First, if pigeons evaluate social contingency directly, a prior expectation for response timing may focus their contingency analysis on a specific temporal window following the initial social signal. Secondly, pigeons may use the temporal contiguity of signal-response relations directly to infer responsiveness, instead of conducting a complex contingency analysis. Either way, if pigeons’ sensitivity to the timing of social contingency reflects response detection mechanisms, our results indicate that signals occurring less than 3s after the initial signal are more likely to be considered as responses than signals occurring over 9s after the initial signal. In other words, partners waiting more than 9s to respond would not be perceived as a responsive partner. The 9s delay may have moved the partner’s response beyond the subject’s window of expectation for that response and therefore the subject may not have been attentive when the response occurred.

Little is known about the neural-cognitive underpinnings of social contingency detection and there is little agreement that the ‘3s boundary’, as suggested by Watson (1966) in his studies on human infants, should be conceptualized as an absolute barrier (Watson 1985, Gergely and Watson 1999). After a signal is emitted, pigeons may well have a broader timeframe, than humans, over which they perceive a partner’s signal to be in response to their own. Such cognitive flexibility would necessarily reflect the natural distribution of pigeon response timing and may be important in detecting social responses that are typical of pigeon courtship.
interactions. An interesting possibility is that both the present findings and Toda and Watanabe’s (2008) findings reflect the same underlying psychological processes for social response detection (see p.46). Their findings showed that when pigeons were trained to discriminate between temporally continuous self-movies (delayed by 0, 3, 5, or 7 s) from non-contingent Playback movies the subjects’ discrimination performance was equally high at delays of 0 or 3s and began to drop-off (but still remained above chance) when delays were increased to 5 or 7 s. This pattern of behaviour across manipulations in the timing of social contingency is congruent with the pattern found in the present study. If Toda and Watanabe’s results and the present results do indeed reflect the same underlying mechanisms for social response detection, then according to Toda and Watanabe’s findings the 3s timeframe may indeed lie just under the boundary for response detection. Had we selected a few more time delays in the 4-7 second range, the boundary for response detection may have become more apparent. Future studies may wish to address this possibility.

It should also be considered that a temporally delayed but still contingent social response might be interpreted differently than if the partner’s behaviour is non-responsive entirely (Striano et al. 2006). Under this interpretation, the potentiation of a male’s behaviour in the 3s delay condition might not reflect his disrupted ability to detect female responsiveness but instead, his reaction to perceiving a delayed response from his female partner. The perception that a female’s responses are delayed but responsive might motivate the male to increase his courtship efforts to grab the female’s wavering attention.

Another possible explanation for the opposite-acting effects of the 3s condition and the 9s condition on male courtship intensity would be the existence of multiple female responses that each exert opposite effects on male courtship intensity and also have different temporal windows that define the male’s response detection. Specifically, the pattern of results in males would occur if the 3s delay selectively disrupts the male’s detection of a female response that normally
decreases his circle walking duration, whereas the 9s delay additionally disrupts the male’s detection of another type of female response that normally potentiates his circle walking behaviour. Some ideas about female signaling patterns that fit with this suggestion will be discussed in greater detail after presenting a post hoc analysis measuring behavioural sensitivity to partner responsiveness (see p.103).

3.6.3.2 Perceptual crossing

Another possible explanation for these results is that the dynamics of pigeon courtship interaction are sensitive to perceptual crossing events. An experimental time delay that is long enough to ‘uncross’ any relevant perceptual crossing events could destabilize the courtship dynamic which, in turn, would affect the circle walking behaviour composing that system. If this explanation is accurate, the results suggest that the relevant perceptual crossing event is comprised of a behaviour that has an average duration between 3 and 9s, since the 9s delay ‘uncrosses’ the perceptual interaction. This time frame rules out many candidates like eye contact, head-bobbing, bowing or the fine spatiotemporal dynamics of circles, since these perceptual crossings would be uncoupled by short, 1 or 3s, time delays. In fact, this timeframe leaves only one obvious behavioural candidate for perceptual crossing: the circle walking bout. Based on these findings, we suggest that a relevant perceptual crossing event in pigeon courtship is simultaneous circle walking (SCW).

The idea of a self-potentiating SCW dynamic represents a mechanistically simple but diversely consequential perceptual crossing process capable of producing interactive behaviour. If the visual cues of circle walking trigger circle walking, when SCW occurs, this event will trigger a mutually congruent social ‘release’ that potentiates circle walking in both pair members at the same time. By bidirectionally potentiating circle walking behaviour, SCW increases the likelihood that SCW will re-occur, over and over again. SCW might be thought of as the most
potent form of social ‘release’ because it triggers a ‘feed-forward’ cycle which can drive coherent, self-potentiating social dynamics in spite of individual or inter-individual variations (Froese et al. 2010). Circle walking behaviour and the SCW dynamic, of course, would reciprocally influence each other. Froese has called this the ‘constitutive autonomy’ of the interaction process where, in this case, there exists a reciprocal dependency between the individual agents’ circle walking behaviour and the overall SCW dynamics of the courtship system (Froese et al. 2007).

In the event that the SCW dynamic between pigeons is disrupted, as in 9s delay and Playback conditions, in any moment that one pigeon becomes motivated to engage, the other animal may be in another social ‘space’, experiencing a different social event altogether. This unshared experience would create a mismatch in the dynamics of mutual influence, thus destroying the stability of SCW dynamics and their influence on individual circle walking duration. When each subject is experiencing a different interaction, SCW can only occur by illusionary coincidence. Even when a pigeon interacts with a convincing illusion of a responsive social partner, the illusionary SCW structure cannot maximize the social coherence of the perception and action dynamic like true SCW dynamics can.

SCW dynamics may also explain the potentiation of male behaviour in the 3s delay condition. We have seen throughout these experiments that male and female pigeons exhibit different patterns of circle walking behaviour; males perform long sustained bouts, whereas females perform many short bouts. Also, as observed in the present experiment, males more commonly adjust their behaviour by modulating their bout duration, whereas females modulate the number of circle walking bouts in their display. The influence of the SCW dynamic on male behaviour may become enhanced in the 3s delay condition because of the way this delay shifts the female’s short circle walking bouts within the context of the male’s longer circle walking bout, as well as the male’s unique way of modulating his courtship intensity. We will elaborate
more on this idea later after presenting a post hoc dyadic analysis of SCW in courtship (see p. 103).

3.6.3.3 Is interactive behaviour specific to courtship?

The findings imply that interactive behaviour may be specific to courtship. Interactive behaviour could be instrumental in achieving two important functions of courtship behaviour: a) to mitigate the negative effects of male aggression on the outcomes of courtship (Tinbergen 1952; Lorenz 1966; Patricelli et al. 2004; Patricelli et al. 2006) and b) to mediate the formation of social preferences and pair bonding by enhancing social motivation and social coherence (Macedonia et al. 1994; D’eath and Dawkins 1996; Kodric-Brown and Nicoletto 1997; Trainor and Basolo 2000; Swaddle et al. 2006). How might the mechanisms of interactive behaviour mediate these functions?

With respect to response detection mechanisms, specific signal-response contingencies may be uniquely adapted to function in courtship. Researchers studying bowerbird (Ptilonorhynchus violaceus) courtship have articulated the female signaling hypothesis which purports that, female signals are a primary force modulating male courtship intensity (Borgia and Presgraves 1998; Borgia and Coleman 2000; Patricelli et al. 2002; Patricelli et al. 2004; Patricelli et al. 2006). The need for female communication lies in the fact that intense, aggressive male display is attractive to females because it conveys information about male fitness but, at the same time, it can be threatening and therefore detrimental to the functions of courtship (Sullivan 1994; Andersson and Iwasa 1996; Borgia and Presgraves 1998). Depending on the circumstance, the same male display might lead to mating or it could startle the female and cause her to flee. To alleviate this uncertainty, specialized female signals are thought have evolved to inform the male about her emotional state. When the female is fearful she signals to reduce the intensity of the male’s display (Patricelli et al. 2004; 2006). When the female feels safe and sexually motivated
she signals to potentiate male courtship intensity, thus gaining greater access to the information contained in his display (Patricelli et al. 2002; Coleman et al. 2004). Such communications are thought to evolve in mating systems where males are aggressive and females are choosy. The result is a cooperative communication where both sexes benefit by enhancing efficacy of courtship (in males) and mate search (in females) (Borgia and Presgraves 1998; Borgia and Coleman 2000; Patricelli et al. 2004; 2006).

The pigeon’s socio-sexual ecology fits the profile for female signals to evolve towards modulating male courtship intensity; male pigeons court aggressively, involving forceful advances and even physical attacks (Goodwin 1983) and female pigeons are choosy (Burley 1983). Thus, the courtship-specificity of interactive behaviour in pigeons may be explained by the existence of communications between female signals and male responses that are sensitive to the manipulation of social contingency.

With respect to perceptual crossing dynamics, SCW dynamics that drive escalated circle walking behaviour may be more consistent in courtship. The feed-forward dynamics that perceptual crossing can elicit depends on mutually congruent responses to be triggered in response to the perceptual crossing event. In rivalry, circle walking interactions are likely to entail a wider variety of social response dynamics; at the beginning of a competition, SCW may trigger mutual display enhancement (as in courtship), but eventually one animal will decline their circle walking behaviour and this non-congruent response dynamic will likely self-perpetuate, just like SCW does, yet in this case one animal’s behaviour will increase and the other’s will decrease. Thus in rivalry, circle walking dynamics are likely to exert more complex, bidirectional effects on circle walking behaviour between partners.
3.6.3.4 Type II error

As implied above, it is possible that interactive behaviour is not specific to courtship. Instead, a different, perhaps more complex, type of interactive behaviour may occur in rivalry interactions that exhibits less sensitivity to the manipulation of social contingency and behavioural assay employed here.

There is diverse evidence for interactive behaviour between rivals other species. In duetting songbirds, for instance, rivals overlap or match their song types and song frequencies (Dabelsteen et al. 1997; McGregor et al. 1992; Peake et al. 2005; Burt and Beecher 2008) to convey specific information about their motivation to defend, attack or submit in competition (Enquist 1985; Todt and Naguib 2000). Male lizards also appear to use their visual display behaviour interactively (Macedonia et al. 1994; Ord and Evans 2002). Using a special technique called interactive video playback, a male Jacky dragon lizard (*Amphibolorus muricatus*) was presented with a rival (on video) whose behaviour was governed by an algorithm: ‘begin an aggressive display bout if no subject display had been detected within the last X seconds, where X is the mean latency of displays in response to a conspecific display’ (Ord and Evans 2002). The lizards behaved differently depending on whether they interacted with an interactive partner or a non-interactive one. Notably, X was very large, 17.5s, compared to the mere seconds that describe the vocal contingencies between songbirds. Therefore it is possible that the contingencies between visually signaling rivals have a uniquely large temporal window in which contingencies can maintain their behavioural relevance, which exceeds our time delay manipulations. Such a long window of responsiveness and response detection would also be particularly vulnerable to the illusions of social contingency and therefore would be robust to the manipulation of social contingency with Playback.
3.6.3.5 Conclusion

The findings of this experiment suggest that the type of interactive circle walking behaviour observed is courtship-specific and sensitive to the temporal contiguity of socially contingent behaviours. The findings did not, however, elucidate a distinction between the potential response detection and perceptual crossing mechanisms underlying interactive behaviour. In order to further understand interactive behaviour and its sensitivity to social timing, the next section presents a post hoc dyadic analysis of the data collected here, in Experiment 4. The new analysis measures partner responsiveness and SCW to examine the role that these social contingencies may play in the pigeon’s interactive behaviour.

3.7 A post hoc dyadic analysis

So far our findings have shown that a pigeon’s circle walking behaviour is interactive during courtship (Experiment 2, 3, 4). Furthermore we found that this form of interactive behaviour does not depend on the social partner’s facing direction (Experiment 3) but does rely on social timing (Experiment 4). Playback conditions and 9s time delays were both found to disrupt the apparent influence of social contingency on circle walking behaviour. And surprisingly, 3s delays potentiated circle walking durations in males.

In trying to understand the mechanisms underlying interactive behaviour, we aim to test two ideas in particular:

1) Pigeons may be sensitive to their partner’s responses within the circle walking dynamic. Specifically, for the purposes of the present analysis, partner responsiveness (PR) is defined as the scenario where the subject is currently circle walking and their partner responds to them with circle walking.

2) Simultaneous circle walking (SCW) may constitute a perceptual crossing dynamic that drives stable, self-sustaining social dynamics in courtship (Froese and Di Paolo 2010; Di
Paolo et al. 2008; Auvray et al. 2009). These SCW dynamics both influence and are influenced by the circle walking behaviour of the interacting birds. Therefore the ‘uncrossing’ of SCW events that occurs during social contingency manipulations may be responsible for the observed effects of social contingency on circle walking behaviour.

We conduct two types of analyses to evaluate the potential role that PR and SCW play in the sensitivity of circle walking behaviour to social contingency. The first analysis is designed to assess whether PR and SCW are sensitive to the manipulation of social contingency of Experiment 4: the Live, 1s, 3s, 9s and Playback conditions. The second analysis evaluates the relationship between the trial-specific effects of social contingency on circle walking and the trial-specific effects of social contingency on PR and SCW. For each experimental trial in conditions which significantly affected circle walking behaviour (3s, 9s and Playback), the contingency effect is defined as the reduction in behaviour (circle walking, PR or SCW) in a given experimental trial with respect to its corresponding Live trial. Regression analyses are used to assess whether the contingency effects on circle walking can be explained by the contingency effects on PR and SCW. The results will help to determine if either PR sensitivity or SCW dynamics can explain the pigeon’s interactive behaviour in courtship.

3.7.1 Methods

3.7.1.1 Data Processing

To measure PR and SCW for each trial in Experiment 4, several steps were conducted. First, the raw motion energy data for each subject in each trial was converted to a 360s time series, where each 1s time bin contains a number indicating whether the subject was circle walking or not. To achieve this, the motion energy values for each 1s time bin were averaged together and this average was labeled as being above or below the motion energy threshold for circle walking (Experiment 1). Second, for each trial each subject’s data series was matched and
temporally aligned to their partner’s data series to represent the interaction as it was experienced by the subject during the trial. Third, each subject’s data series was combined with their partner’s data series to yield a single data series where each 1s time bin indicated one of four possible dyadic events: A) the subject circled alone, B) the partner circled alone, C) the partners circled together (SCW), or D) neither bird circled. Finally, PR and SCW were measured. PR was taken as the number of times that A was followed by C, i.e. when the subject’s partner joined in with a subject-initiated circle walking bout. For SCW, the total duration, average bout duration and total number of SCW bouts were measured.

3.7.1.2 Analysis

Two types of analyses were conducted. The first assessed whether PR and SCW varied across the five contingency conditions of Experiment 4 (Live, 1s 3s, 9s and Playback). For PR, a single 2-way repeated measures ANOVA [2 (sex) x 5 (contingency)] was performed. In finding an interaction between social contingency and sex, two 1-way repeated measures ANOVAs [5 (contingency)] were conducted to test the effects of social contingency in each sex separately. Sex was treated as a between subjects factor, social contingency as a within subjects factor and subject was treated as the random variable (N = 18).

For SCW, three 1-way repeated measures ANOVAs [5 (contingency)] were performed to evaluate the effects of social contingency on each of the three measures of SCW (total duration, average bout duration, and number of bouts). Note that sex was not a factor due to the inherent sexual symmetry of the SCW measure. Social contingency was treated as a within subjects factor and subject was treated as the random variable (N = 18). An alpha level of .05 was used to evaluate significance in all ANOVAs.

For all ANOVAs yielding significant effects, four pairwise t-tests were used to compare the 1s, 3s, 9s and Playback condition with the Live condition. A Bonferroni corrected alpha of
.0125 was used to evaluate significance. In finding p < .05, the effect was identified as being marginally significant.

The second analysis was designed to assess the role that PR and SCW played in the contingency effects on circle walking behaviour. Only the data from the experimental conditions that had a significant effect on circle walking behaviour (3s, 9s and Playback conditions) were included in the analysis. To reiterate, the contingency effect is defined as the reduction in behaviour (circle walking, PR or SCW) in a given experimental trial with respect to its corresponding Live trial (e.g. contingency effect on circle walking = circle walking in Live – circle walking in experimental condition). The contingency effects on circle walking behaviour were regressed against the contingency effects on PR and SCW using a linear regression analysis. For SCW data, both sexes were analyzed together as one data set, given the inherent sexual symmetry in the SCW measure. Since only three conditions were analyzed from the 540 trials of Experiment 4, \( n = 322 \). For PR, the male and female data were analyzed separately, since PR and the effects on PR across experimental conditions are found to be sexually asymmetric in the PR ANOVA (described above). For each sex \( n = 161 \).

Since the contingency effects on PR and SCW both necessarily correlate with the contingency effects on circle walking behaviour by chance, a measure of this chance relationship is required to evaluate whether the observed relationship differs from the chance relationship. To accomplish this, ‘random PR’ and ‘random SCW’ data was created by pairing each subject in each trial with a partner from a randomly selected trial, matched for experimental condition and social context. The relationships between the contingency effects on circle walking and the contingency effects on random PR and random SCW were evaluated using linear regression analyses. T-tests were used to assess whether the slope of the regression trend line for the real pairs differed from the slope of the regression trend line for random pairs. The \( t \) statistic is
computed as the difference between the two slopes divided by the standard error of the difference between the slopes on \((n - 4)\) degrees of freedom. (Meng et al. 1992; Howell 2007).

3.7.2 Results

3.7.2.1 Partner responsiveness

In the results of the ANOVA analysis, the effect of social contingency on PR significantly interacted with subject sex, \(F(4, 64) = 4.41, p = .003\). For males, there was a significant effect of social contingency on PR, \(F(4, 64) = 18.01, p = .001\), which can be explained by significant differences in PR between the Live and 9s conditions, \(t(8) = 3.73, p = .006\), and between the Live and Playback conditions, \((t(8) = 3.42, p = .009)\). There was no effect of social contingency on female PR, see Figure 12.

![Figure 12](image-url)

**Figure 12. The effect of social contingency on partner responsiveness**

The experience of partner responsiveness, the event that the subject’s partner responds to the subject’s circle walking bout with circle walking behaviour, differs significantly across the social contingency conditions in Experiment 4 for males only. The black asterisk (*) indicates a significant difference between the marked condition and the Live condition \((p < .0125)\). \(L = \text{Live}, P = \text{Playback} \text{ and } 1s, 3s \text{ and } 9s \text{ are time delay conditions.}

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The regression analysis showed that in females, the contingency effects on PR significantly predicted the contingency effects on circle walking scores in real pairs, $B = 7.01, t(160) = 10.79, p < .001$, and in randomly paired birds $B = 4.26, t(160) = 8.502, p < .001$. The contingency effects on PR also explained a significant proportion of variance in the contingency effects on circle walking in real pairs, $R^2 = 0.355, F(1, 160) = 116.56, p < .001$, as well as in randomly paired birds, $R^2 = 0.251, F(1, 160) = 72.28, p < .001$. For females, the slope of the regression line for real pairs is significantly higher than that for random pairs, $t(157) = 3.35, p < .001$. This means that, for females, the relationship between the contingency effects on circle walking and the contingency effects on PR is significantly greater than chance.

For males, the slope of the trend line for the relationship between the contingency effect on circle walking and the contingency effect on PR is significant for real pairs, $B = 2.17, t(160) = 10.7, p < .001$, and for random pairs, $B = 2.44, t(160) = 8.50, p < .001$. However, the difference between these slopes in males was not significant (Figure 13). This means that, for males the relationship between contingency effects on circle walking and the contingency effects on PR is not significantly greater than chance.
Figure 13. The relationship between contingency effects on circle walking and contingency effects on partner responsiveness

The figure shows the relationship between the contingency effects on circle walking and the contingency effects on partner responsiveness for female (gray dots, solid gray line) and male subjects (black dots, solid black line). The random pairs were created for assessing the chance relationship between the contingency effects on circle walking and the contingency effects on partner responsiveness in females (dashed gray line) and male subjects (dashed black line). The data points for the random pairs are not shown in the diagram. The difference between the slopes for real and random pairs is significant for females but not for males, suggesting that partner responsiveness is relevant to female circle walking behaviour.

3.7.2.2 Simultaneous circle walking

The effect of social contingency on total SCW duration is significant, \( F(4, 64) = 9.22, p < .001 \), which can be explained by significant differences between the Live and 9s conditions, \( t(17) = 5.84, p < .001 \), and between the Live and Playback conditions, \( t(17) = 4.14, p = .001 \).

The effect of social contingency on average SCW bout duration data was significant, \( F(4, 64) = 5.51, p < .001 \), which can be explained by a marginally significant difference between the Live and 3s conditions, \( t(17) = -2.177, p = .018 \).
The effect of social contingency on the number of SCW bouts was significant, $F(4, 64) = 23.38, p < .001$, which can be attributed to significant differences between the Live and 9s conditions, $t(17) = 5.91, p < .001$, and between the Live and Playback conditions, $t(17) = 3.45, p = .003$ (Figure 14).

![Figure 14](image.png)

**Figure 14. The effect of social contingency on simultaneous circle walking in courtship**

Simultaneous circle walking, the event that a male and female pigeon engage in circle walking at the same time, differs significantly across the social contingency conditions presented in Experiment 4. The black asterisk (✳️) indicates a significant difference between the marked condition and the Live condition ($p < .0125$). The gray asterisk (☆) indicates a marginally significant difference ($p < .05$). L = Live, P = Playback and 1s, 3s and 9s are time delay conditions.

The results of the regression analysis showed that the contingency effects on SCW significantly predicted the contingency effects on circle walking scores in real pairs, $B = .74, t(322) = 13.77, p < .001$, and randomly paired birds, $B = .27, t(322) = 5.16, p < .001$. The contingency effects on SCW also explained a significant proportion of variance in the contingency effects on circle walking in real pairs, $R^2 = 0.311, F(1, 322) = 189.67, p < .001$, as well as in randomly paired birds, $R^2 = 0.06, F(1, 322) = 26.66, p < .001$. The slope of the regression line for real pairs is significantly higher than that for random pairs, $t(318) = 6.29, p <$
.001. This means that, for both sexes, the relationship between the contingency effects on circle walking and the contingency effects on SCW is significantly greater than chance. See Figure 15.

Figure 15. The relationship between contingency effects on circle walking and contingency effects on partner responsiveness

The relationship between the contingency effects on circle walking and the contingency effects on simultaneous circle walking (black dots, solid black line) and male subjects (black dots, solid black line). The random pairs were created for assessing the chance relationship between the contingency effects on circle walking and the contingency effects on simultaneous circle walking (dashed black line). The data points for the random pairs are not shown in the diagram. The difference between the slopes for real and random pairs is significant, suggesting that simultaneous circle walking is relevant to circle walking behaviour.

3.7.3 Discussion

The results of this analysis support the idea that the pigeon’s interactive behaviour can be explained by behavioural sensitivity to PR and SCW. We found that female circle walking, but not male’s, may be sensitive to PR whereas both sexes circle walking behaviour appears to be sensitive to SCW.
Before considering the results in detail, it is useful to briefly discuss what was discovered about the dynamics of pigeon courtship. One distinct characteristic is a pronounced sex difference in the way males and females engage in the courtship dynamic. The male is usually the initiator of circle walking and the female usually responds to the male, thereby creating SCW. During a six minute session, males experience PR 18 times on average (i.e., the female joins in to his circle walking display with circle walking), whereas females experience PR only 5 times on average. The best way to conceive of pigeon courtship then, may be to view male circle walking behaviour as an overarching architecture - a structural scaffolding within which the female joins in to create SCW – and to view female behaviour as a ‘pacemaker’ that drives and determines the fine structure and timing of SCW dynamics. Nearly 65% of all female circle walking is spent engaged with her partner in SCW, while just 37% of male circle walking behaviour takes place during SCW bouts.

3.7.3.1 Female response sensitivity

In the context of the courtship dynamic described above, the female pigeon’s sensitivity to PR is particularly meaningful because for females, PR (when the male follows her circle walking with circle walking) is relatively rare. To appreciate this result one must consider the whole sequence of events leading up to the measured PR event: 1) the male courts aggressively, 2) the male pauses his courtship display, 3) the female re-initiates circle walking and 4) the male responds with circle walking. While only the last step in this sequence was measured, PR implies the existence of this whole interaction sequence.

The female signaling hypothesis (see p. 100) - that female signals may be an important force modulating male courtship intensity (Patricelli et al. 2002; Borgia and Presgraves 1998; Borgia and Coleman 2000) - may help explain the sequence of interaction described above. This hypothesis predicts that females exhibit two types of signaling behaviour (Patricelli et al. 2006).
One female signal would be designed to trigger an increase in male display, functioning to gain greater access to the male’s fitness information when the female feels sexually motivated. In the pigeon, the female’s circle walking behaviour would be an obvious candidate to fulfill this function. Another female signal would be designed to trigger a decrease in male circle walking when the female feels threatened, functioning to mitigate the damages of male aggression on the outcomes of the female’s mate search; a responsive male would also benefit by improving the efficacy of his courtship display (Patricelli et al. 2006; Borgia et al. 2000). Such an ‘appeasement’ signal could elicit a pause in the male’s display, moving the interaction sequence described above from step 1 to step 2. We suggest this signal may be the head nod.

The head-nod is a rapid gesture that does not extend as low as bowing behaviour but is deeper than head bobbing. Goodwin (1983) suggests that head-nodding derives from a nest-building gesture and is the pigeon’s equivalent of saying "here I intend to nest", a message that can be hostile, defensive, inviting or suggestive, according to the social circumstances. Wosegien and Lamprecht (1989) showed that head nodding appeases male aggression. They used the human fist to mimic the head-nodding action, while recording male subjects’ aggressive pecks towards the nodding hand. They found that the nodding action reduces the number of aggressive male pecks towards the hand both immediately and progressively over repeated trials, as compared to the control situation in which the hand was rotated horizontally instead of ‘nodding’ vertically (Wosegien and Lamprecht 1989). Throughout all the experiments presented in this thesis, females were frequently observed to head nod and we suggest that the function of head nods in this context may lie in appeasing male circle walking intensity.

When social contingency is manipulated, a head nodding female would no longer be capable of successfully appeasing male display. The male would continue to circle walk and the female would remain in a defensive state. This would result in a reduction of female circle walking duration as observed in the results of Experiment 4.
3.7.3.2 Male response sensitivity

The absence of male sensitivity to PR may be explained by the complexity of female signaling dynamics. If female head nods act to decrease male courtship duration, the disruption of head nodding contingencies would result in an increase of male circle walking durations. On the other hand, if female circle walks act to potentiate male courtship duration, the disruption of female circle walking contingencies would result in a decrease of male circle walking durations. It is possible that these effects cancel each other out when relating the contingency effects of circle walking to the contingency effect on PR in the regression analysis. It is also possible that these different social contingencies with opposite acting effects on male behaviour explain the male’s increased circle walking in the 3s condition and his decreased circle walking in the 9s and Playback conditions. Conceivably, the 3s delay condition might specifically disrupt the influence of female head nodding signals on male behaviour, whereas the 9s delay and Playback conditions additionally disrupt the influence of female circle walking on male behaviour. In the 9s delay and Playback conditions the effects of disrupting female circle walking signals on male behaviour, may overpower the opposite-acting effect of disrupting head nodding signals, especially given the role of female circle walking responses in the formation of SCW.

It is important to note that evidence for female or male PR sensitivity does not necessarily imply response detection, that the pigeon is ‘aware’ that their partner’s actions are in response to her own, or, that the pigeon uses these responses psychologically (perhaps ‘unconsciously’) as social feedback. While the pigeon’s ability for recognizing a partner’s displays as responses is possible, there are other alternative explanations for the PR sensitivity observed. The contingency sensitivity of the social dynamics that are set up between female head-nodding, female circle walking and male circle walking modulations could also explain the observed experimental effects without implying the existence of complex psychological mechanisms for response detection. Perhaps if the definition of perceptual crossing is considered...
more loosely, to include interactions between sexually dimorphic perceptions and sex-specific responses, the interactive nature of the communication between female signals and male display could be explained by social dynamics alone.

3.7.3.3 SCW dynamics

The findings support the idea that SCW triggers a self-perpetuating perceptual crossing dynamic. Specifically, the decrease in circle walking behaviour from the Live condition to the 9s and Playback conditions appears to be explained by the fact that SCW is ‘uncrossed’ and the perceptual crossing dynamic breaks down. This results in the destruction of the potentiating effects that SCW dynamics have on individual circle walking behaviour. In fact, SCW is even more sensitive than individual circle walking behaviour to the manipulation of social contingency; SCW drops almost 30% from the Live to the 9s delay condition (Figure 14), whereas individual circle walking only drops 15% between these conditions. This observation, together with the strong relationship observed between the contingency effects on SCW and the contingency effects on circle walking (Figure 15), provides convincing evidence that the interactive behaviour of pigeons can be explained, in large part, by SCW dynamics.

SCW dynamics also lend an explanation for the potentiating effect that the 3s delay has on male behaviour. The sex specificity of this effect may lie in the fact that males potentiate their circle walking differently than females do. Males typically add circles to bouts, whereas females perform short bouts more frequently. The 3s delay is not long enough to uncross and breakdown SCW dynamics because the overarching structure of SCW is determined by the males’ long circle walking bout, which lasts much longer than 3s. Instead of uncoupling SCW, the 3s delay would have the effect of delaying the temporal position of female responses as they occur within the male’s display behaviour. This could influence the process of male bout termination or initiation. If male bout termination depends on placement of female circle walking within the male bout,
under the 3s conditions, the male pigeon would receive this stimulation later, causing him to extend his circle walking bout a little longer. Also, females viewing a delayed male bout, may respond to his display after he has terminated it, causing him to re-initiate his next bout a little sooner. On the other hand, females modulate their display intensity by producing a greater number of short bouts, and this form of behavioural modulation might be less sensitive to the effects of the 3s time delay circle walking duration.

3.7.3.4 Conclusion

The pigeon’s sensitivity to PR and SCW during courtship interactions both present plausible explanations for the emergence of interactive circle walking behaviour in pigeons. It remains unclear however, if the female’s PR sensitivity is the result of specialized psychological processes for detecting responsiveness or if PR sensitivity can be explained by mechanisms inherent in the system dynamics of courtship. If both psychological and systems level mechanisms are acting to create interactive circle walking behaviour, they almost certainly develop, function and influence behaviour in an inter-dependent fashion. Indeed, a ‘co-function’ between these mechanisms might make it very difficult to tease these processes apart, even if the ‘ideal’ experiments could be conducted. Using the naturalistic experimental paradigm employed here, it is simply impossible to tease the effects of psychology and social dynamics apart.

The finding of female’s PR sensitivity suggests that the female signaling hypothesis (Patricelli et al. 2004; Borgia and Presgraves 1998; Borgia and Coleman 2000) may be a useful framework for explaining the interactive dynamics of pigeon courtship. In future work, investigating social contingencies that have opposite-acting effects on subject behaviour may prove to be extremely practical for separating and studying the effects of different social contingencies on behaviour. Thus, the suggested bi-directional influence of female circle walking
and head-nodding signals on male courtship intensity would be a good behavioural model to focus on.

The data also strongly support the SCW dynamics hypothesis; representing possibly the first empirical demonstration of a dynamic systems approach to explaining social contingency sensitivity in a natural social interaction (see DiPaolo et al. 2008; Auvray et al. 2009; Froese and Di Paolo 2010; De Jaegher and Froese 2009). Since the theoretical frameworks for perceptual crossing dynamics has only very recently been developed, it currently lacks empirical support in complex natural systems, methods for investigating these processes and practical behavioural models in which to study them (Di Paolo et al. 2008). The pigeon model presents a particularly exciting opportunity for study in this area.

The most valuable contribution of the experiments presented in this thesis, is perhaps in demonstrating the richness and complexity of the social dynamics emerging from the visual communications of this species. The pigeon’s courtship interaction, described earlier as ‘unspectacular’ compared to visual duetting species, appears to be a sophisticated rule-based interactive dynamic that is ideal as a model for interactive visual communication in the field of behavioural neuroscience. While the findings of this thesis work have perhaps provided more questions than answers, it has become obvious that the opportunity for discovery about social interactivity with this particular animal model is wide ranging. In particular, exploring the possibility of multiple mechanisms underlying interactive courtship, as well as the neural basis and function of these mechanisms is an exciting goal for future research.

The concluding chapter of this thesis suggests a theoretical framework that may be helpful for researchers studying social interactivity. Three classes of mechanisms for interactive behaviour are considered, which are conceived to occur through three different ‘levels’ of behavioural influence: system dynamics, perception and cognition.
Chapter 4

Social Dynamics or Interactive Psychology? Towards Understanding the Mechanisms of Interactive Social Behaviour

The pigeon’s courtship behaviour is socially interactive; it is determined not only by immediately preceding visual stimulation, but also by the relations between a bird’s own actions and those of its courtship partner (Experiment 2). Using spatial and time delay manipulations (Experiment 3, Experiment 4), we were able to narrow down the list of social contingencies that might potentially influence pigeon circle walking behaviour. The findings of a post hoc analysis of the data obtained in Experiment 4 supported the idea that simultaneous circle walking (SCW) and partner responsiveness are relevant in pigeon courtship. We suggest that SCW can be described as a perceptual crossing event, as described by recent work with dynamical systems models of social interaction (Di Paolo et al. 2008; Froese and Di Paolo 2008; Froese and Di Paolo 2010). During SCW, both pigeons become simultaneously stimulated by their partner’s circle walking display and both pigeons congruently react by potentiating their circle walking behaviour. This SCW dynamic increases the likelihood that SCW itself will re-occur and, of course, also increases the duration and frequency of circle walking behaviour composing SCW. The post hoc analysis also indicated that female circle walking behaviour is sensitive to the male’s circle walking that occurs in response to her own circle walking behaviour. This led us to speculate that pigeon courtship dynamics behave according to the predictions of the female signaling hypothesis (Patricelli et al. 2002; Patricelli et al. 2004; Patricelli et al. 2006; Royle and Pike 2010). The basic tenet is that female signals function to modulate male courtship intensity to enhance the efficacy of the female’s mate assessment (Patricelli et al. 2004). Responsive males also benefit from this communication by enhancing the efficacy of their courtship
behaviour. We hypothesize that female pigeon’s possess two types of signals: one, circle walking, that functions to elicit an increase in male courtship intensity (and the female’s access to male fitness information) and another signal, head nodding, that appeases aggressive male display (as demonstrated by Wosegien and Lamprecht 1989). These courtship communications would help to maximize the transfer of fitness information and to avoid female startling (Patricelli et al. 2002).

The findings provide a basis for further developing the pigeon as a model for interactive visual communication. The direction that such an investigation could take critically depends on the ‘level’ of social interaction – individual psychology (Watson 1985) vs. the system of social dynamics (Di Paolo 2008; Auvray 2009) – that contains the mechanisms underlying interactive social behaviour. The main goal of this final chapter is to put forward a revised theoretical framework for classifying the potential mechanisms underlying interactive behaviour. The hope is that in using this framework, scientists can better formulate a comprehensive approach to the study of social interactivity.

4.1 Three mechanisms for interactive behaviour

The framework begins with what can now be considered the most basic class of mechanism: perceptual crossing, a dynamic process at the systems level of social interaction.

1) The mechanism of perceptual crossing, at this point, is best described as being shaped by two stages: a) the event that two perceptual activities of the same nature simultaneously interact, as in eye contact, mutual touch or simultaneous action (like SCW in the pigeon) (Di Paolo et al. 2008; Auvray et al. 2009) and b) a mutually congruent response dynamic, which describes the visuo-motor transformations of both animals that link social stimulation to their subsequent behaviour. Congruent response patterns potentiate the likelihood that the initial perceptual crossing event will re-occur. And, in this way, the perceptual crossing dynamic self-perpetuates itself in such a way that is diversely interconnected with the quality of social
coherence and fitness outcomes of the ensuing social dynamic. Perceptual crossing mechanisms are distinct in that they do not imply the existence of any psychological/neural substrates at the ‘individual level’ that are specialized for detecting or evaluating signal relations. The rich information contained in perceptual crossing dynamics, however, may provide a basis for the evolution of interactive psychology.

The next two classes of mechanisms constitute what we refer to here as interactive psychology. This term, interactive psychology, has been used throughout this thesis to distinguish specialized brain mechanisms that evaluate social relations and produce interactive behaviour from the perceptual crossing dynamics described above, from which interactive behaviour simply ‘emerges’ from mutually triggered signal response dynamics. Unlike perceptual crossing dynamics, interactive psychological mechanisms serve adaptive behavioural functions like assessing the quality of communications and learning to improve the performance of reward driven social behaviour.

2) Here we introduce the term interactive multisensory integration (IMI). IMI is conceived to describe a set of mechanisms which integrate the individual’s kinaesthetic sense of their own social signals with their visual experience of a conspecific’s signals. The kinaesthetic senses underlie the sensation of one’s own body movements and are thought to involve the sense of one’s position in space (somatosensory) and the sense of one’s motor effort (somatomotor) (Proske and Gandevia 2009) The idea of IMI is inspired by recent work showing that multisensory integration between various senses (somatosensory, visual, auditory etc.) is a common theme of neural function (Meredith and Stein. 1986; Allman et al. 2009; Stein et al. 1988). In social interaction, integration between the kinaesthetic senses for evaluating self-action and the visual evaluation of other’s action could equip the organism with a superficial sense of social coherence to afford the perception, evaluation and discrimination of such qualities. But, such multisensory integration would not necessarily imply the ability to detect partner responses
as being related to one’s own, or to use social feedback for learning. IMI mechanisms may explain a variety of phenomena, such as duets, interactional synchrony in humans and other varieties of mutual displays, in which individuals appear to sense information about ‘social togetherness’ but do not necessarily possess the ability to process and use information about the causal relations between signals. The pigeon, for example would benefit from evolving the ability to sense the degree and quality of SCW within their interactions. Given the rich information that this event contains about the quality and ensuing dynamics of the courtship interaction, pigeons possessing IMI mechanisms might achieve better mate choices and higher reproductive fitness. And, perhaps there are other, yet to be discovered, behaviourally meaningful temporal and spatial qualities of social interaction for which pigeons have evolved to sense.

3) Social feedback mechanisms are conceived to be a class of cognitive mechanisms that afford the use of social responses in learning to signal more efficiently. In registering social responses as ‘reward’ or ‘punishment’, this feedback ‘informs’ the agent about the consequences of their own reward-driven behaviour, which consequently enables adaptive modification of and control over that behaviour. It is possible that pigeons use partner responses as social feedback. In particular, we presented evidence that the female may be sensitive to male responsiveness, specifically, in the way that the male modulates his circle walking behaviour in response to female signals. If males or females experience their partner’s responses as reward (e.g. male modulations, female circle walks) or punishment (e.g. male non-responsiveness, female head nodding), this feedback might act to potentiate behaviour that leads to positive reinforcing social outcomes and decrease behaviour that leads to negative ‘punishing’ social outcomes. By using social feedback to inform their developing social strategies, pigeons could improve their mate search and courtship strategies and, ultimately, increase their reproductive fitness.

Before further detailing this framework it is useful to highlight and explain the changes made to the pre-existing framework (that has been used up to this point) for describing the
mechanisms of interactive behaviour (Chapter 1). Most prominently, the classification and terminology used for the psychological mechanisms of interactive behaviour are revised. Previously, for referring to the psychological mechanisms underlying the animal’s ability to process conspecific signals as being causally related to its own (articulated by Watson et al. 1966, 1986, 1985, 1999, 2000, 2001), we used the term response detection. It now seems appropriate to delineate two types of psychological mechanisms, one perceptual and one cognitive. We suggest a class of perceptual mechanism, IMI, which may help explain phenomena in which subjects appear to possess a superficial sense of social coherence, but not an ability to process the specific response dynamics between signals.

The idea that an interactive perceptual mechanism may underlie an animal’s behavioural sensitivity to social contingencies is not entirely new. Gergely and Watson’s (1999) described the ability to perceive the timing, spacing and other relational qualities between socially contingent events as being part of a perceptual-cognitive ‘toolkit’ for social contingency detection. A major difference between the IMI mechanism proposed here and Gergely and Watson’s model, however, is that Gergely and Watson conceived that such perceptual mechanisms were ultimately employed in ‘social contingency detection’ to ‘understand’ partner responses and use them as feedback. We suggest that interactive perceptual mechanisms may exist, IMI mechanisms, that do not necessarily function in processing the causal relations between signals and responses, but only creates a superficial ‘feeling’ of partner responsiveness or social ‘togetherness’. These mechanisms would necessarily be multisensory in order to integrate the animal’s sensation of self-action with their perception of another’s actions.

For the cognitive mechanism, which is most closely related to Watson’s ‘contingency detection toolkit’ (1985), the term social feedback processing is suggested here to replace the terminology that has been used in the past, such as social contingency detection (e.g. Gergely 2000), social contingency perception (e.g. Watson 2000) and response detection (as used in the
The new name is chosen because it emphasizes the purported capability and function of such a mechanism in using information about partner responses as they relate to the individual’s own behavior to enable social learning. This name however does not make any inferences about the use of a specific mechanism or ability – such as social contingency analysis or response detection - to achieve this function.

Finally, notice that we have changed the order in which the classes of mechanisms are presented. Up to this point, the psychological mechanisms (Watson 1985) and the social dynamical mechanisms (Di Paolo 2008; Auvray 2009) have been presented and discussed in the order that they have appeared in the scientific literature. In a new framework, it is more appropriate to discuss social dynamics first, since perceptual crossing mechanisms should be considered as a more fundamental set of social processes which would necessarily predispose and shape the evolution of psychological mechanisms for interactive behaviour.

To clarify the new framework, Table 3 presents the major distinctions between perceptual crossing dynamics, interactive multisensory integration and social feedback processing.

The next section discusses each of these three mechanisms in greater depth. The final section reviews work in behavioural neuroscience that can lend insight into the neural basis of psychological mechanisms for interactive social behaviour: IMI and social feedback processing.
Table 3. Three mechanisms for interactive behaviour

<table>
<thead>
<tr>
<th>Mechanism producing interactive behaviour:</th>
<th>1 Perceptual crossing dynamics</th>
<th>2 Interactive multisensory integration</th>
<th>3 Social feedback processing (response detection)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Level:</td>
<td>Social dynamics</td>
<td>Interactive psychology Perception</td>
<td>Interactive psychology Cognition</td>
</tr>
<tr>
<td>Description of mechanism:</td>
<td>Congruent sensory-motor ‘release’</td>
<td>Kinesthetic - visual sensory integration</td>
<td>Operant (reward) and classical (associative) conditioning</td>
</tr>
<tr>
<td>Behavioural function:</td>
<td>None</td>
<td>Evaluating social coherence and communication quality</td>
<td>Learning to optimize and control social behaviour</td>
</tr>
<tr>
<td>Possible sensitivities in pigeons:</td>
<td>SCW</td>
<td>SCW, inter-signal timing and spacing</td>
<td>Partner responses: ♀CW ↔ ♀CW ♀HN ↔ ♀CW</td>
</tr>
</tbody>
</table>

4.1.1 Perceptual crossing

Much is to be gained from describing the perceptual crossing dynamics emerging from social interaction and it is exciting that the field of animal behaviour has barely begun to explore this potential. At the psychological level, a set of ‘straightforward’ stimulus-release processes are sufficient to create perceptual crossing events that can give rise to interactive social behaviour. Essentially, the same dynamical processes that drive simple coordinated phenomena like synchronizing pendulums or Walter’s ‘dancing’ robots can also explain the emergent interactive coherence between a wide range of social behaviours like people’s moods, habits, actions and ideas (Walter 1950a; Walter 1950b; Kugler et al. 1980; Kelso 1995; Miles 2009; Ouillier, 2005;
Enquist, 2002; Sebanz et al. 2006). The pigeon’s circle walking interaction, of course, is no exception.

Dynamical processes can act to coordinate behaviour under a variety of circumstances, even in the presence of noisy fluctuations, behavioural asymmetries and individual differences (Di Paolo 2000). They should be considered unique to each species, social context, pair combination and social interaction. To explain each unique social dynamic with a general template, one might describe the processes by which the perceptual crossing dynamic is shaped, can escalate, break down and repair ‘itself’. In the following paragraphs, these concepts are used to offer a detailed description of the social dynamics in pigeon courtship.

4.1.1.1 Shaping the perceptual crossing dynamic

Since the male pigeon’s circle walking bouts are longer than the female’s, the male’s behaviour predominantly defines the global structure of the courtship interaction. It is therefore useful to think of the rhythm in male circle walking as forming a dynamic foundation within which the patterns of the social interaction unfold. The continuous cycloidal trajectory of the male’s circle walk represents a potentially potent force shaping perceptual dynamics, since circles, when performed continuously, produce rhythm. The cyclical dynamics of male display will also introduce rhythm into his perception of the dynamic visual cues given by his female partner. Rhythmic perception, in turn, would manifest in rhythmically triggered response behaviour within the male’s circle walking display. Together, the male’s rhythmic display, rhythmic perception and rhythmic response behaviour define a pronounced rhythmic structure framing the perceptual crossing dynamic in courtship.

4.1.1.2 Escalation

Due to the rhythmic structure in male courtship, of course, a female viewing the male’s courtship display also receives rhythmic visual input, which triggers a rhythmic pattern of activity
in her visually triggered behaviour. A female’s behaviour is rhythmic by itself but to a lesser degree than that of the male, because female circle walking bouts are short, sporadic and produce less of a continuous cycloidal rhythm. The visuo-motor ‘release’ of female circle walking might be considered more complex and ‘choosy’ than that of the male. When the female does respond to male courtship she initiates SCW, which can be described as a perceptual crossing event. Her response creates a socially congruent ‘checkpoint’ where both pigeons’ visuo-motor processes are aligned. The ensuing dynamics are coherent, which drives the patterns of behaviour into an ordered state of temporal and spatial agreement (Di Paolo 2000). In this way, SCW sustains itself in an escalating, feed-forward dynamic which is constitutive of the circle walking behaviour making up SCW (Froese 2010). Since the female usually initiates SCW, female behaviour can be conceived as a driving ‘pacemaker’ for the escalation of courtship dynamics, progressing towards higher and higher levels of social coherence.

4.1.1.3 Breakage and repair

If the female becomes fearful of male aggression, she stops circle walking and social coherence breaks down. A cooperative female would signal her fearful state, perhaps with a head-nodding signal. There are two possible outcomes to this event which depend on the male’s ensuing actions. First, the male could maintain his intense aggressive manner. In this scenario the female would likely disengage from courtship, run away and this particular pair would not likely ever engage in a reproductive relationship. Alternatively, the male could pause his circle walking behaviour. In doing so, the male suspends the threatening stimulus so that the female’s fear can dissipate. A cooperative female would then cue the male of her refreshed state with a circle. If the male has not lost his motivation, he will re-join in courtship, possibly with a modified intensity level to avoid startling the female once again. Through this cooperative series of signals and responses, the courtship interaction is ‘reset’, social coherence is repaired and the
mating opportunity is restored. Some might also regard female pauses and head-nodding signals as a coy strategy designed to test and assess the male’s responsiveness and commitment to the relationship (Wickler 1980; Smith 1994; Wachtmeister and Enquist. 1999).

4.1.1.4 Information in perceptual crossing dynamics

Why would an animal evolve psychology for sensing perceptual crossing events? As we have seen in pigeons, there is a bidirectional relationship between the coherence of perceptual crossing (driven by SCW) and the duration of circle walking composing those dynamics which are both likely to predict fitness-related social outcomes. Together, perceptual crossing, social coherence and the motivated behaviour composing the interaction are tightly interconnected, and can be predictive of a diverse array of social information. Only pairs that are mutually motivated, mutually attracted, perceptually attuned, mutually attentive (Smith 1994) and dynamically compatible will be capable of coherent interactions that progress towards mutual approach, dynamic coherence and its repair, pair bonding, mating and reproduction. Thus, the coherence of social dynamics might be used as a heuristic to evaluate one’s partner and the potential success of a future partnership. Perceptual crossing dynamics are also critically related to the efficacy of communication. A perceptually coordinated courtship will enable better transmission of the information contained in the courtship display. The quality of perceptual coordination in courtship may predict the efficacy of communication in the future as well. For instance, perceptually and dynamically compatible pair combinations should be more likely than less coherent pairs to achieve better reproductive synchrony (Cheng 1992) territorial defense (Hall and Peters 2008), mutual mate guarding and protection (Lovell-Mansbridge and Birdhead 1998; Grafe and Bitz 2004) nest building, foraging and parenting. The ability to sense the diverse information connected with perceptual crossing dynamics would be an enormous fitness advantage, especially in monogamous species where the choice of a mate will influence the
individual’s fitness throughout the duration of his or her entire lifetime. Throughout evolution, mechanisms for evaluating perceptual crossing dynamics in courtship would be selected because individuals that can evaluate perceptual crossing dynamics would conduct more efficient mate searches, make better mate choices, achieve better communication, and ultimately, maintain greater reproductive fitness.

### 4.1.2 Interactive multisensory integration

The ubiquity of multisensory signaling and multisensory processing in animal communication is becoming increasingly recognized as a pervasive trend in social neuroscience. The brain appears to place increased salience value on events that evoke stimulation in more than one modality (Bro-Jørgensen 2009; Bravery 2007; Otovic and Partan 2009; Fusani, 2007). Perhaps paying attention to events that evoke multiple and different sensations at once, inherently cues the animal’s attention to the most relevant events in their environment. Such multisensory events may be more reliable and valid indicators of behavioural relevance, as compared to a single cue occurring alone. The brain’s tendency to emphasize the saliency of multisensory events has been described as *multisensory response enhancement*: the process by which the integration of two stimuli presented in separate modalities together elicit an enhanced neural and behavioural reaction compared to when either stimulus is presented alone (Stein et al. 1988). For instance, in pigeons the female’s response to male audio/video playbacks is more vigorous than her combined response to either audio or video stimulus presented alone (Partan et al. 2005). The view that various brain modalities are extensively interconnected has gained momentum due to single cell recording studies of multisensory neurons that integrate various combinations of sight, sound, touch and kinaesthetic sensations (Meredith et al. 1986; Stein et al. 1988; Allman 2009; Holmes 2005, 2005; Nagy, 2006; Perrett et al. 1985; Pellegrino et al. 1992). In current theories of brain function, multisensory integration is no longer considered the mere result of a late convergence of
the senses in so-called associative areas of the brain, but rather as a dynamical organization emerging from the coupling of otherwise segregated sensory processing areas (Calvert et al. 2004; Kelso 1995).

Here we suggest the possibility of interactive multisensory integration, a specialized type of multisensory integration for social interaction. In the case of IMI in visual communication, kinaesthetic cues associated with self-motion and visual cues associated with viewing another animal’s movement are integrated. Under this view, interactive behaviour might be explained, in part, by multisensory enhancement, where responses towards co-occurring self-display and partner display are greater than to either stimulus presented alone.

The effects of multisensory enhancement on neuronal and behavioural reactions (Meredith and Stein 1986; Partan et al. 2005; Nagy et al. 2006; Zahar et al. 2009) have been described as following a few simple (but ‘loose’) rules. Multisensory enhancement is most likely to occur when stimuli from different sensory modalities come from approximately the same spatial location, (the spatial rule), when they occur at approximately the same time (the temporal rule), and/or when at least one of the two stimuli is by itself only weakly effective in stimulating the response (the inverse effectiveness rule) (Holmes and Spence 2005).

In considering these rules in the context of IMI, there are clearly unique computational problems associated with integrating sensory information about self and other during social interaction. Recall the mirror problem, introduced in Chapter 1(see p.11); the lack of direct sensory correspondence between the kinaesthetic representation of self-action and the visual representation of a partner’s behavior. A defining characteristic of IMI mechanisms may be in broadening the spatial and temporal rules of multisensory enhancement to ‘solve’ the mirror problem by adapting the ‘rules’ of enhancement to fit the parameters typical to social contingencies. The invariance in the temporal and spatial relational profiles of signal-response relations and perceptual crossing events affords the evolution of reliable temporal and spatial
integration rules that are adapted specifically to integrate information between successive signals in social interaction.

4.1.2.1 The functionality of IMI

With IMI mechanisms, social animals could sense the quality of communication – i.e. the degree of reciprocal responsiveness, mutual motivation, perceptual crossing and mutual attunement - without deeply understanding the causal relations between signals. For instance, humans in conversations with high levels of interactional synchrony report greater feelings of social rapport and ‘togetherness’ (see p.13). People seem to sense the dynamic qualities of their communications, but cannot identify or ‘pinpoint’ any specific events or causal relations that give rise to these social impressions (Tickle-Degnen and Rosenthal 1990; Bernieri et al. 1996; Grammer et al. 1998).

Similarly, in order to explain the evolution of duetting or other forms of coordinated mutual display, a mechanism for perceiving social dynamics, such as IMI, seems absolutely necessary. In duets, the temporal and spatial ‘rules’ of multisensory enhancement are, essentially, ritualized. In visual duets for instance, perceptual crossing seems to be exaggerated in synchronous movements and in vocal duets the dynamic between signals and responses is scripted and rapidly executed. The quality of these ritualized dynamics is then evaluated to make decisions about mate choice, territorial defense and mate guarding (Hall 2003). Such signals could not have evolved into a ritualized form unless the signal receivers possessed some form of psychology to reliably evaluate the information contained in these signals (Guilford and Dawkins 1991), and we suggest that IMI may represent such a mechanism. Furthermore, the fact that duetting has evolved in many phylogenetically diverse avian taxa (Malacarne et al. 1991) implies that a basic perceptual mechanism for sensing social dynamics, which necessarily preceded the evolved exaggeration of this trait, may be widespread across avian taxa.
The idea that organisms might use interactive multisensory ‘perceptual heuristics’ to sense partner responsiveness has been considered previously with respect to the social contingency detection and the social feedback learning framework (Watson 2000). Watson suggested that animals use the timing, spacing and other relational qualities between signals to infer that those signals are causally related. But, the idea that animals might use temporal or spatial integration to gain a sense of perceptual crossing events has not yet been considered. So far, perceptual crossing has only been conceived as a mechanism for producing interactive behaviour at the ‘system’s level’ of social dynamics (Di Paolo et al. 2008; Auvray et al. 2009). However, given that perceptual crossing dynamics can predict ensuing social dynamics and social outcomes, it would be highly adaptive for social animals to evolve heightened perception, memory and responses that exploit this information. In pigeons, for instance, it would be adaptive to experience enhanced perception, memory of and responses towards SCW, since SCW is predictive of the pair’s ensuing social dynamics and duration of the interaction.

The purported function of IMI in sensing perceptual crossing events can be loosely considered, though with cautious speculation, through the lens of one’s own experience of events like eye contact (Argyle and Dean 1965; Chapman 1975), kissing, handshakes or other ‘crossed actions’ like simultaneous smiling, laughing, crying, running or dancing. Even abstract coincidences like winning together, losing together, or being in the same park at the same time of night might be conceived loosely as a perceptual crossing event. Anecdotally, perceptual crossing events are both salient and integral in creating a sense of shared experience with another person.

To review, the idea of IMI is purely hypothetical; however, we argue that such speculation is useful for several reasons. For one, the evolution of mechanisms for sensing social dynamics is greatly afforded by the invaluable information contained in them. Second, IMI is conceived as a specialized form of a well-documented, straightforward and widespread neural
mechanism (multisensory integration). Third, IMI might resolve a number of unexplained phenomena like the evolution of coordinated mutual displays and the relationship between interactional synchrony and perceived rapport in humans. Fourth, IMI does not make any claims about complex cognitive abilities in non-human subject species that have been so controversial in the past, like the possession of goal-driven, strategic social behaviour. Lastly, the IMI model complements and may provide an important basis for, the better known, yet still ill-understood, cognitive model for interactive psychology.

4.1.3 The social feedback mechanism

A fundamental feature defining the behaviour of any dynamic system is whether it can be described as an open-loop or closed-loop process. Social feedback is the process by which part of output of the signaler’s motor command is returned to the signaler’s sensory system in order to regulate the signaler’s motor system, thereby ‘closing the loop’ of social interaction (Beer 1995; Wolpert 2003; Scott 2004).

4.1.3.1 Learning through social feedback

By developing hypotheses, or ‘expectancies’ about a partner’s responses, the signaler is enabled to strategically modify their own behaviour in order to test and learn effective signaling strategies across varying social contexts. A signal’s consequences can depend on the recipient’s sex, dominance, familiarity, age, facing direction, behavioural state, recent history, spatial position (distance, territories, conspecifics etc.), as well as on hidden variables like the receiver’s attentional state, motivational state, sexual attraction, their social rank or their social ‘personality’, like their tendency to react sexually, aggressively, fearfully, quickly or cautiously. Social feedback processing enables the opportunity to optimize the outcomes of interaction by discovering this information through trial and error learning.
Learning through social feedback can occur by the same mechanisms by which animals learn to peck or press a key for food rewards or to avoid a hurtful shock in operant conditioning paradigms. The reward or punishment acts as a source of feedback and behavior can be adjusted to repeat actions leading to reward and discard actions which lead to punishment (Bolles 1972). Social behaviour may be adjusted in the same way, but in response to social stimuli that elicit sensations of reward or punishment.

In an operant conditioning paradigm, Gilbertson (1975) showed that, for male pigeons, female stimuli do not solely act to ‘trigger’ a reflexive courtship response, but that female stimuli are rewarding in and of themselves. Male pigeons could be trained to peck a key when that action was paired (‘rewarded’) with a brief presentation of a female conspecific. Essentially, the male ‘works’ to view the female by modifying his behaviour in novel ways (Gilbertson 1975). Animals can also learn associations between arbitrary environmental cues and social events and use these associations to guide adaptive social behaviour. For instance, male pigeons that were exposed to arbitrary environmental cues (light, sound) followed by a brief display of a female partner, eventually began courting in response to the environmental cue alone (Rackham 1971, cited in Gilbertson 1975). It is not a far stretch to conceive that in natural situations, pigeons can modify their social behaviour based on action-outcome feedback and environmental-outcome associations.

4.1.3.2 Getting feedback from social contingencies

The major difference between natural social dynamics and many operant conditioning paradigms is the contingency schedule upon which rewards are received. Social contingencies are unique in their degree of statistical, temporal and spatial variation. Epstein, Lanza and Skinner (1980) demonstrated that pigeons learn even when the reward schedule is governed by a conspecific agent, thereby creating a truly ‘social’ schedule of action-outcome contingencies.
These researchers trained two pigeons, Jack and Jill, to ‘symbolically communicate’ with one another, and to learn by food rewards that were released by one another’s response behaviour. Jack and Jill’s final performance is described as a sustained and natural ‘conversation’. In short, Jack ‘asks’ Jill with a key press for trial-specific information regarding which key to press to receive a food reward. After Jack’s prompt, Jill looks through a trap door at an illuminated colour key and gives the correct ‘answer’ to Jack by pressing a symbolic name key, Jack receives the symbol, rewards Jill by pressing a ‘thank you key’ (rewarding Jill with food), decodes the given symbol to select the correct colour key and receives his food reward. Although this is a highly trained and artificial ‘social’ interaction, the experiment demonstrates operant learning that is based on a contingency schedule directly regulated by a conspecific social partner. The experiment, therefore, would have a similar interactive response dynamic to natural pigeon interactions (Epstein, Lanza and Skinner 1980).

Some authors have suggested that the unique dynamic of social interactions – that is partially unpredictable, but partially under the control of the animal - may be rewarding in and of itself (Werner and Latane 1974). The propensities of an innate attraction to the contingency schedules characteristic of social dynamics would explain several observed phenomenon: for example, quail chicks imprint more readily on socially contingent adults (Ten Cate 1986), house pets appear to actively seek out social reciprocity and attention through play (Werner and Latane 1974) and human infants prefer the same (Gergely 2000; Bigelow 2001). If social dynamics are rewarding, subjects may modify their behaviour to repeat behaviours that elicit a ‘feeling of reward’, promoting behaviours that tend to produce rewarding social dynamics and discarding those that do not. In pigeon courtship, the subject’s sense of social coherence might facilitate longer circle walking bouts because the social dynamic, in itself, is fundamentally rewarding and behaviourally reinforcing.
4.1.3.3 The use of social feedback in courtship

If animals can be trained to key peck to trigger the appearance of a conspecific display in an operant chamber (Gilbertson 1975), a logical implication is that they can also learn to modulate their behaviour using social feedback in natural social situations. One type of communication that would greatly benefit from social feedback learning is that articulated in the female signaling hypothesis (see p.100): the idea that, in courtship, female signals act to modulate male courtship display, a communication which benefits both male and female fitness outcomes (Patricelli’s 2002, 2004, 2006). Royle and Pike (2010) for instance suggest that a male zebra finch (*Taeniopygia guttata*) learns about his own attractiveness from female social feedback; he increases his display only when female feedback encourages him to do so. These researchers manipulated males to appear more or less attractive (using different colours of leg bands), and tested their courtship behaviour in response to a female who could either see the male (across clear glass) or could not see the male (across one-way glass). The attractive males increased their courtship intensity over the trial, but only if they could learn how ‘sexy’ they were from a female partner who could view and respond towards him (Royle and Pike 2010).

The possibility that animals get ‘skilled’ at signaling and responding efficiently over time is supported by documentation of behavioural development in bowerbirds (*Ptilonorhynchus violaceus*). In bowerbirds, more experienced females are more tolerant of intense male display, are less likely to become startled and therefore achieve more accurate mate assessments (Patricelli et al. 2004). More experienced males are more responsive to female signals and succeed more in mating (Patricelli et al. 2002). One explanation is that through social feedback learning, experienced bowerbirds have shaped more effective signaling behaviour, thereby refining their ability to strategically control and optimize the interaction (Uy et al. 2000; Uy et al. 2001; Patricelli et al. 2004).
There seems to be nothing ‘magical’ about using social feedback to learn new and effective behavioural strategies. Such learning occurs by the same mechanisms underlying operant learning, where rewarded behaviours tend to be repeated and unrewarded or punished behaviors tend to be discarded. It is well documented that pigeons can learn in operant chambers and there is no obvious reason why learning social expectancies through natural social rewards would be an exception. The only difference between social learning and operant learning is that social learning entails a slightly unpredictable contingency schedule, which, according to some, might actually be rewarding in and of itself (Werner and Latane 1974; Bigelow 2001).

### 4.2 The neural substrates of interactive psychology in birds

Whether an animal species is equipped with interactive psychology is perhaps most conclusively answered by examining the neural substrates underlying social interactivity. Are the brain mechanisms of sensory-motor ‘release’ connected with other neural loci that integrate information about social dynamics (e.g. multisensory integration areas, reward systems)?

Currently, finding answers to this question is difficult, not only because of the overwhelming number and complexity of the neural connections necessarily involved, but also because the research area of social neuroscience is still in its infancy. The expansive brain networks underlying social dynamics are still poorly understood. Fortunately, a working understanding of avian brain structure and function is growing at a steady pace (Reiner et al. 2004; Shimizu 2009; Akutagawa and Konishi 2010). The pigeon brain in particular, has been, and will continue to be, used as a prominent model and source of reference (e.g. (Atoji and Wild 2009; Patton et al. 2009; Xiao and Frost 2009; Karten and Hodos 1967).

#### 4.2.1 The substrates of social vision

Just as vision for high speed flight provides a constant informational flow for guiding motor decisions (Wasserman et al. 1988; Cook 2001), social vision might best be conceived as
providing a continuous flow of social information that guides social reactions and responses. The avian brain has two main visual pathways. The tectofugal pathway leads through the optic tectum of the midbrain, through the nucleus rotundus of the thalamus (nRt) and to the entopallium (E) (Bischof and Watanabe 1997). The thalamofugal pathway projects from the retina, to a dorsal nucleus in the thalamus towards the hyperpallial visual Wulst (Karten et al. 1973; Güntürkün and Hahmann 1999).

4.2.1.1 Pathways for social vision

The tectofugal pathway, subserving the bulk of ‘primary’ visual processing, appears to be arborized into several functional ‘streams’ that process different visual features in parallel. This ‘featural’ topography begins at the level of the nRt, which is composed of several feature-specific regions that are specialized for processing luminance, colour, object motion and optic flow (Wang et al. 1993; Hellmann and Güntürkün 2001). The nRt projects to the E which retains much of the nRt’s topography while also integrating some visual features into a more complex representation (Husband and Shimizu 1999). For example, the E contains areas combining optic flow and object motion (Xiao and Frost 2009). Lesions in the E have been shown to impair a pigeon’s ability to visually discriminate individual conspecifics but do not hinder their ability to discriminate conspecifics from heterospecifics (Watanabe 1992). Watanabe suggests that a visual feature integrated in the lesioned entopallial area is used in identifying conspecifics. Such parallel featural processing has prompted comparisons between the avian tectofugal pathways and the major bifurcation of object and motion processing in the primate brain, commonly known as the ‘what and where’ visual pathways (Goodale and Milner 1992; Nguyen et al. 2004; Shimizu et al. 2010).
Beyond the strictly visual areas of the brain, visual 'association' areas (VAAs) can be loosely defined as brain regions that integrate visual information with cognitive processes and other sensory information (Patton et al. 2009). In a recent study, Patton, Husband and Shimizu (2009) identified three VAAs that activate in the brain of a male pigeon while he interacts with a female. These VAAs include the lateral portion of the intermediate nidopallium (NIL), the medial nidopallium (mN) and an area of the visual Wulst, the hyperpallium apicale (HA). All three areas are diversely interconnected with each other, as well as with other parts of the pallium (Husband and Shimizu 1999; Atoji and Wild 2009; Wild 1987).

In fact, Patton (2009) showed that these VAAs activated differentially depending on whether the female presented was a socially contingent or non-contingent partner. Specifically, their contingent condition (Live) involved interaction with a female across clear glass, so that the
male and female could both see and hear each other. Their non-contingent condition (Playback) involved the presentation of a prerecorded female pigeon on video playback. Thus, it is important to recognize that, in addition to social contingency, the Live and Playback stimuli also varied in visual quality (which was distorted in video conditions), as well in the presence of auditory stimulation (present in live conditions). Still, one explanation for the differences in the gene expression of mN, NIL and HA is that some of this activity underlies psychological processes, like IMI or social feedback processing, that lead to interactive social behaviour in pigeons.

The NIL is a direct extension of the tectofugal visual pathway projecting from E and may be involved in processing conspecific movement (Lieshoff et al. 2004; Sadananda and Bischof 2006; Patton et al. 2009). In the primate visual system, the ‘object’ and ‘motion’ pathways converge in regions of the temporal cortex containing cells that bind form and motion information and respond to classes of dynamically moving objects: an inherently social category, which primarily includes conspecific display (Perrett et al. 1985; Pellegrino et al. 1992). A compelling possibility is that the NIL in the avian brain also represents a region binding social form and motion. Since this area is primarily visual, Patton et al. suggests that the differential activation observed in NIL may have been due to the differences in video quality across conditions, rather than to the presence or absence of social contingency in the male’s interaction. It is also possible that the NIL, being a ‘higher order visual area’, does not function discriminately towards ‘lower level’ visual qualities that occur aberrantly on video (like colour or luminance), but rather responds to the holistic visual ‘concept’ that defines a courting conspecific. The male’s concept of a female partner might even include features of social dynamics like perceptual crossing and social responsiveness. For example, the human brain area known for its role in processing ‘biological motion’ (the posterior part of superior temporal sulcus), appears to be sensitive to the interactive quality of a social stimulus (Blakemore et al. 2003), but not so sensitive to the visual
details of the stimulus (Thompson et al. 2005). While this is purely speculative, a role for NIL in assessing the relations between social signals (and guiding interactive behaviour) cannot be completely ruled out. Since NIL is primarily an extension of the visual pathways, this area would be a likely candidate for IMI to occur via its connections with modalities involved in kinaesthetic perception (somatosensory/somatomotor cortices) (Wild 1987).

The mN is a multisensory association area that integrates auditory, somatosensory and visual stimuli (Jarvis et al. 1998; Kruse et al. 2004). Known for its role in social imprinting (Metzger et al. 1996), mN is thought to integrate the multisensory stimuli associated with conspecifics (Lieshoff et al. 2004; Sadananda and Bischof 2006; Patton et al. 2009). Patton et al. suggest that activity in the male pigeon’s mN may have discriminated Live and Playback conditions based on the presence of auditory cues in the Live condition. Again, until a controlled experiment is conducted the possibility that this multisensory area plays a role in processing social contingencies, especially as a center for IMI, should not be ruled out.

The HA is highly integrated with the Wulst, a structure known for its function in visual cognition (Medina and Reiner 2000). The structure and function of the Wulst, including the possession of primary visual, somatomotor and somatosensory areas has invited comparisons of this pallial structure with the mammalian neocortex (Wild 1987; Funke 1989; Medina and Reiner 2000). Patton and his colleagues suggest that, of the brain regions discriminating between the Live and Playback conditions, HA is the most likely to be related to the interactive qualities of social interaction, by way of its role in reward learning. Lesions in the HA have been shown to produce learning deficits, not in learning acquisition, but in learning reward reversals (i.e., adjusting behaviour when experimenters change the reward schedule reinforcing behaviour) (MacPhail and Reilly 1983; Shimizu and Hodos 1989; Watanabe 2003). HA, therefore, does not appear to be critical in the initial acquisition of action-outcome ‘expectancies’ (Bolles 1972), the experience of reward or the visual processing of and attention to reward-related stimuli. Rather,
HA may play a role in flexibly adjusting and ‘reversing’ the associations made between visual stimuli, behavior and reward outcomes (Shimizu and Hodos 1989; MacPhail, 1983; Watanabe 2003; Bingman et al. 2008). Supporting this idea, Bingman (2008) found that single neuronal responses in HA become sensitive to specific S+ (positively reinforced stimuli) and S- (negatively reinforced stimuli) during reversal learning. In a social context, the HA of zebra finches activated in response to a first courtship experience as well as the presentation of a nest box condition, suggesting that the HA functions to mediate the association between arousal and a variety of stimulus types, including social ones (Sadananda and Bischof 2006).

Taking this evidence together, it seems likely that, during courtship interactions, the HA acts in associating social signals and social responses with motivational reward outcomes. The HA may function by binding the arousal elicited by a partner’s response to the somatomotor cues associated with performing the social signal eliciting that response, as well as to environmental cues that help predict that response. Such a mechanism could mediate social feedback learning; where a signaler would learn to re-iterate social signals that previously led to rewarding social responses and to discard behaviours that did not.

4.2.2 The visuo-motor interface

It is well known that pigeon circle walking behaviour is heavily guided by visual input (Frost and Troje 1998; Shimizu 1998; Patton et al. 2003; Partan et al. 2005; Watanabe and Troje 2006). Åkerman (1965) demonstrated the neural basis of these visual ‘social release’ mechanisms when he electrically stimulated regions of the pigeon’s pallium (including VAAs). The pallial stimulation elicited bowing, cooing and circle walking, but did so to a lesser and more variable degree than direct stimulation to the preoptic area of the hypothalamus, a brain area that elicits motivated circle walking behaviours via its connection to the motor system. Åkerman’s
results imply a top-down influence of pallial regions, including areas processing visual cues, on ‘lower’ brain structures that organize sexual display behaviour.

At the center of the brain networks subserving multisensory control over motor behaviour are the basal ganglia (BG). The BG ‘funnel’ and integrate massive pallial inputs, working closely with the limbic system (Thompson et al. 1998; Cheng et al. 1999; Carr et al. 2003) and motivational reward systems of the midbrain (Veenman et al. 1995; Goodson et al. 2009) to control adaptive social behaviour. In the pigeon, Åkerman (1965) observed multisensory enhancement on circle walking intensity when he stimulated the subject’s lateral striatum (lSt), a large BG input nucleus, while simultaneously presenting that subject with conspecific visual stimulation. The lSt receives major projections from somatotopic areas, somatomotor areas (Zeier and Karten 1971) and VAAs including NIL (Veenman et al. 1995; Medina and Reiner 1997). The lSt, therefore, appears to be in position for the multisensory integration of stimuli associated with both self-action and a conspecific’s display. The position of this structure, along with Åkerman’s evidence for (social) multisensory enhancement in this area, together present exciting evidence that the lSt could be directly involved in IMI.

4.2.2.1 Neuromodulation

Surrounding the BG, there exists a distributed system of sex-steroid sensitive areas, which are commonly referred to under the umbrella of the term motivation areas (MAs): areas that act together with the BG and the thalamus to control the motor execution of sexual behavior and other behaviours motivated by reward (Goodson et al. 2005; 2009). The MAs include a) parts of the hypothalamus: the preoptic area of the hypothalamus (pOA) (Balthazart and Ball 2007), the posterior medial hypothalamus (PMH) (analogous to ventral part, VMH, in mammals) (Cohen and Cheng 1981) b) limbic areas like the ‘avian amygdala’, nucleus taeniae (nTn) (Cheng et al. 1999), the hippocampus (Taziaux et al. 2007) and the nucleus accumbens and c) midbrain areas
such as the midbrain central gray (avian homolog of the periaqueductal gray), the ventral tegmental area (VTA), substantia nigra, bed nucleus of the stria terminalis (BST) and lateral septal nuclei (Goodson et al. 2005). The presence of a conspecific is associated with a distinct pattern of activation across these MA nodes (Goodson et al. 2005; 2009) which, in turn, has a widespread neuromodulatory influence on spinal and neuromuscular pathways that control social behaviour (Schlinger et al. 2001), as well as pallial regions subserving sensory perception and motor planning (Alger et al. 2009). The neuromodulatory influences projecting from MAs include many varieties of specialized chemicals like dopamine, serotonin, aromatase, vasotocin, estrogen, testosterone and nitric oxide, to name just a few (Goodson 2005; Schlinger et al. 2001; Panzica et al. 2006). These neuromodulatory projections are highly specialized: functionally catered to produce a diversity of rapid or slow, locally targeted or distributed, long term or short term neuroplasticities that influence sensory and motor function (e.g. Remage-Healey et al. 2008).

Many of these MAs are anatomically and/or functionally sexually dimorphic and these sex differences correspond to distinct male/female behavioural phenotypes. In general, male sexual behaviour, including courtship behaviours, is thought to be predominantly controlled by the pOA, while female typical behaviours are mostly dependent on the PMH (Åkerman 1965; Gibson and Cheng 1979). It is clear, however, that both brain areas have some role in the sexual behaviour of both sexes (e.g. Bernstein et al. 1993).

Considering the sheer diversity of MAs in the avian brain and their role in the sensation of reward and punishment, it seems likely that such a system could support a social feedback learning system that enables a great degree of plasticity in both behaviour and perception. Experiments in quails (*Coturnix japonica*) have shown that the MAs controlling sexual display are modulated depending on the reward-related outcomes of social interaction (Taziaux et al. 2007; 2008). For instance, activity in the male pOA and BST in response to a female quail depends on whether the male’s previous experiences with that female had led to copulation.
(Taziaux et al. 2008). Also, male quails that learn associations between arbitrary stimuli (CS) and sexual reinforcement (a female) show changes in nTn (analogous to the mammalian amygdala) and hippocampus activity during later presentations of the CS alone (Taziaux et al. 2007). Taken together, changes in MA activity appear to be highly sensitive to the multisensory associations made during social interaction. Generating social expectancies for contingencies between the subject’s own behaviour, the sexual partner’s behaviour, environment cues and the rewards associated with social outcomes appear to be a likely functionality of MA activity.

4.2.2.2 Closing the loop

So far we have reviewed the visual pathways processing social stimuli, culminating in pallial VAAs and the integrative descent of this information into the BG, which works closely with MAs to activate the motor regions responsible for social behaviour. The flexibility and adaptability of this system largely depends on whether or not the information processing that occurs at lower areas of the brain (e.g. BG, MAs) feeds back to the pallial regions that control ‘higher order’ perception and action planning (Wolpert et al. 2003; Scott 2004). This type of closed-loop processing is known to occur in anterior forebrain pathways (AFPs): integrative, iterative, recursive, self-referential neural circuits that can act to flexibly adjust the substrates of social behaviour and social perception online, i.e. during action execution (Scott 2004; Nottebohm et al. 1976; Bottjer and Johnson 1997; Burt et al. 2000). AFPs are thought be fundamental in the fine-tuned control and execution of motor behaviour (Kawato et al. 1987; Toni and Passingham 1999) tool use (Berti and Frassinetti 2000; Obayashi et al. 2001), perception, cognition and learning (Csillag 1999; Middleton and Strick 2000; Yin et al. 2005) and social behaviour (Graybiel 2005; Stepanek and Doupe 2010).

The thalamus is considered by many as the key structure ‘closing the AFP loop’ in what can be described as a pallio-BG-thalamo-pallial circuit (Vates and Vicario 1997; Williams and
Vicario 1993). The thalamic ‘relay’ centre acts as the final bottleneck in the informational ‘funnel’ of the BG by sending highly processed information back to pallium as feedback (Parent and Hazrati 1995). In the pigeon, there is some evidence that thalamic nuclei may be involved in relaying information during social interaction (Wild 1994; Atoji and Wild 2009). Specifically, the caudal part of the dorsolateral posterior thalamic nucleus (DLPc), which receives visual and somatomotor input, has been suggested to be analogous to nucleus uvaeformis of songbirds (Wild 1994). In the songbird, this nucleus is thought to integrate information during social interaction in order to control the precise timing of song execution within the dynamic context of the vocal interaction (Williams and Vicario 1993). If the pigeon DLPc is indeed analogous in function to the songbird nucleus uvaeformis, this structure might function in fine-tuning the timing and execution of the circle walking display according to the dynamics of courtship.

The MAs of the brain may be another source of pallial feedback. A recent study has shown that pOA activity in songbirds has widespread pallial projections targeting the nuclei of the song control system (Alger et al. 2009). Lesioning the pOA hinders sexually motivated song, an effect which is thought to be due to the disruption of reward priming in regions controlling social behaviour and social vision. The author, Alger, suggests that the pOA acts to organize and coordinate activity between motor areas subserving song production and multisensory areas that process social sensory information (e.g. VAAs).

Although the functional roles of both the thalamic nucleus DLPc and pOA in the pigeon are much less understood than the analogous songbird structures, it is compelling to speculate that MAs like the pOA and/or a thalamic relay center like DLPc might function recursively during social interaction to control the coordination between motor planning and perceptual processing. Such an AFP could attune behaviour to the social consequences of action and equip the organism for social feedback learning. Much more research into the pigeon’s brain and behaviour would
have to occur to substantiate such a conjecture and one should not disregard this possibility until these brain systems are investigated more thoroughly.

In developing the pigeon as a model for visual communication, there is much to gain from theoretical models of motor control and the songbird model. Theoretical models of motor control have advanced the idea that the brain can learn about the sensory consequences of action and utilize this information to control the sensory consequences of future actions, rather than allowing behaviour to become a ‘slave’ to the sensory stimulation in the environment (Wolpert et al. 2003). The songbird model has become the leading model for understanding these processes in vocal communications (Yanagihara and Hessler 2006; Huang and Hessler 2008; Kao et al. 2008). The pigeon model has the potential to do the same for the study of non-verbal communication. However, since the neuroscience of social behaviour in the pigeon has yet to approach a level of description which affords a comprehensive discussion of the substrates underlying interactive social behaviour, examples from research in the songbird brain are useful here to exemplify the sophisticated function of circuits enabling social behavioural control.

4.2.2.3 Examples of AFPs for song control

A basic appreciation of how the AFP for song control works is assisted by introducing the concept of stochastic variability. Stochastic variability is the quality of ‘randomness’ that characterizes cell firing patterns in parts of the AFP pathway (Kao et al. 2005; Kao et al. 2008). The function of stochastic cell firing has been recently described in the lateral magnocellular nucleus of the anterior nidopallium (LMAN), a multisensory ‘motor planning’ and sensory integration area (Kao et al. 2005; Kao et al. 2008). The stochastic bursting of LMAN cells appears to underlie innovative song execution, where a subject can the flexibly adjust and test their songs in a ‘trial and error’ fashion (Brainard and Doupe 2000; Kao et al. 2005). Critically, LMAN pre-motor activity is only stochastic while a songbird is practicing, but never while he
performs towards a female audience. When song is directed towards a female, the premotor activity of LMAN cells fire precisely in single spikes; this firing pattern is thought to correspond to the ‘best’ up-to-date version of the male’s song (Kao et al. 2005; Kao et al. 2008). After a note is sung towards a female listener the ‘post-motor’ activity of LMAN cells exhibit a stochastic firing pattern, which is thought to be associated with synaptic plasticity (Kao et al. 2008). Conceivably, since this type of plasticity is unique to social interaction with a female, the changes occurring in LMAN circuitry may be directly related to the social feedback provided in female responses. The LMAN plasticity that occurs during interaction with a female appears to shift the ‘pre-motor’ cell firing patterns (that occur later during song practice) towards variations that were previously successful in eliciting female responsiveness (Kao et al. 2008). On the other hand, the plasticity that occurs during song practice is thought to occur directly in motor nuclei to fine tune motor execution using feedback from the bird’s own song (Andalman and Fee 2009).

Another area, area X in the striatal part of the BG, plays a major role in connecting LMAN to the rest of the AFP and is heavily modulated via dopaminergic VTA projections (Sasaki et al. 2006). This dopaminergic modulation depends on the presence of a social partner (Sasaki et al. 2006; Yanagihara and Hessler 2006; Heimovics and Ritzers 2008). The exact function of area X is not well understood but the area’s activity appears to correlate closely with song timing (Goldberg et al. 2010). Also, considering area X’s position in the BG, a major multisensory integrative centre receiving distributed pallial inputs and projecting to the thalamus as well as MA’s (Castelino et al. 2007; Goldberg et al. 2010), area X is ideally placed as a center for integrating information about song interactions, perhaps with IMI mechanisms, to regulate sexual motivation and song tempo in relation to the social dynamics of the interaction.

The activity of brain derived estrogen is another type of neuromodulation that is uniquely active during interactions with a social partner (Gibson and Cheng 1979; Gahr et al. 1993; Harding 2004; Remage-Healey et al. 2008; Remage-Healey et al. 2010). Estrogen acts on the
caudomedial nidopallium, an auditory region related to song learning, song preference and song recognition (Remage-Healey et al. 2008; Remage-Healey et al. 2010). It is conceivable that this type of neuromodulation, being specific to conditions of social interaction and occurring in a sensory association area, could drive flexible attention to and evaluation of social contingency and social coherence in the interaction (Remage-Healey et al. 2010). Such mechanisms would be expected to be especially developed in duetting songbirds that appear to possess sophisticated sensitivities to the temporal precision of social dynamics.

The rapid and targeted neuromodulatory induction of plasticity in brain areas planning and perceiving song is impressive to say the least. Future work in this area has the potential to elucidate much of the ‘interactive code’ within animal interactions by providing insights that can be impossible to achieve using behavioural studies alone. Furthermore, the emerging evidence that the responses of social partners may act as feedback to modulate rapid brain changes in regions related to song planning and perception is enticing evidence for the idea that sophisticated social feedback processing can underlie interactive social behaviour in non-human animals (e.g. Remage-Healey et al. 2010; Goldberg et al. 2010; Heimovics and Ritter 2008; Kao et al. 2008; Andalman and Fee 2009). Such a conjecture has previously been met with much controversy (Marler and Evans 1996; Craig, 1918; Dickinson and Balleine 1994).

In vocal communication, research has advanced to a point where we can actually observe and understand how flexible closed circuit brain systems may be working to control social interaction. Similar systems are likely to subserve visual communications as well. Scientists have yet to utilize the technology that affords the observation of the real time brain function for the purpose of understanding visual communications. Thus, for the pigeon, and other visually communicating species, the connections underlying a potential ‘system of social control’ are yet to be mapped out and understood. In conjunction with the lack of knowledge about how visual communication behaviour might develop over time, this unchartered territory presents an exciting
opportunity for discovery. Although there is no hard evidence about how the pigeon’s courtship display develops throughout their lifespan, anecdotally, social behaviour appears to become more controlled and efficient as individuals gain social experience. Juvenile males appear to court and display with unbridled enthusiasm, only to be attacked by superior males and scare away females. For example, one of the young males that was originally selected for the study, but later had to be cut, showed the typical characteristics of an immature juvenile, courting all the time, sometimes without breaks for the whole six minute trial. This male was clearly not dominant, nor did he appear to successfully attract females. When the animals get older, there is an observable emergence of context appropriate, efficient courtship behaviour. Such development could well be learned and controlled by rewarding and punishing social feedback from conspecifics. Like in the song bird, the brain activity underlying pigeon circle walking behaviour might shift depending on whether the animal is directing the display towards a social partner or not. Such socially-driven ‘activity shifts’ might reflect the development of context dependent, ‘appropriate’ and well-timed courtship displays. A premotor area in the pigeon’s brain that becomes active during courtship and that exhibits plasticity with social experience is yet to be discovered. Yet, with the emerging evidence of the special role that visual cues play in learning (see p.34) and with the observation that many birds continuously develop more adaptive context dependence and flexibility in their visual communication behaviour (see p.33): investigating the role of social feedback processing in the brains of visually communicating species, like the pigeon, represents an exciting opportunity for understanding these phenomena.

4.2.2.4 Solving the mirror problem

So far we have discussed evidence for neuroplasticity that is rapidly driven by a partner’s feedback during social interaction in motor planning areas (Kao et al, 2005, 2008), regions of the BG (Yanagihara and Hessler 2006; Heimovics and Riters 2008) and perceptual parts of the brain
These mechanisms may provide a solution to the mirror problem (see p.11); where achieving correspondence between the disparate brain activity processing self-action and the perception of another’s action is computationally problematic.

One solution to the mirror problem would be to model the social consequences of action, not in terms of the sensory details of a partner’s responses, but rather in terms of the motivational feedback that is elicited by the partner’s response behaviour. Neuromodulatory projections from the pOA VTA, and even from within the pallium itself (Remage-Healey et al. 2008; Alger et al. 200; Yanagihara and Hessler 2006), may function to coordinate activity between separate sensory and motor brain regions thereby achieving correspondence between the motivational undertones of self and other action.

What these neuromodulatory systems do not provide, however, is the ability to precisely code the correspondence between specific actions and the specific sensory details of responses with a high degree of precision. The most precise correspondence between signaling and perceiving responses would require visual information to be integrated into motor areas, containing the most highly detailed ‘high resolution’ representation of action. Neurons that exhibit such integration capacities have been discovered in the monkey motor cortex (Pellegrino et al. 1992). These neurons were named mirror neurons, to refer to their properties of precise visuo-motor correspondence in response to either the perception of action or the performance of action. When the monkey views another monkey’s actions, mirror neurons respond with the same firing pattern that would occur if the monkey performed that same action themselves (Gallese et al. 1996). Recently, mirror neurons were discovered in swamp sparrows (*Melospiza georgiana*) in the HVC of the nidopallium (abbreviation used as proper name, Reiner 2004), a brain area directly connected to the motor substrates subserving song execution. These cells produce identical neural responses whether the bird is singing itself or listening to playbacks of their own or similar songs (Prather et al. 2008).
The most frequently suggested function of mirror neurons is the facilitation of action perception, action identification and action understanding by processing another individual’s actions self-referentially, through the same pathways that the subject uses to engage in those actions themselves (Gallese and Goldman 1998; Rizzolatti et al. 2001; Iacoboni et al. 2005; Prather et al. 2008; Ferrari et al. 2005; de Lange et al. 2008). A design that includes mirror neurons could also serve the functions of interactive behaviour: in detecting and evaluating the relations between one’s own behaviour and that of a social partner. With a mirror neuron the brain could essentially code social contingencies, their probabilistic relations, timing, spatial relations and other relational qualities, directly at the single cell level. A role in processing social contingencies is not usually given as a suggested function of mirror neurons. Instead, the function of action perception and understanding is often used to infer a link between mirror neuron activity with complex social processes like empathy, ‘theory of mind’: the ability to what another individual is ‘feeling’ or ‘thinking’ (Gallese et al. 2001; Schulte-Ruther et al. 2007; Iacoboni et al. 2005). This logic has proven controversial, a debate that might be partially resolved by identifying a more basic function of mirror neurons that may have preceded the evolution of their involvement in more sophisticated functions like developing a ‘theory of mind’. The simple multisensory integration of causally connected events in social interaction as in IMI or social feedback processing may be a potentially important, previously overlooked and more basic function of mirror neurons, from which more complex social functions might have arisen.

The recent discovery of mirror neurons in an avian species opens up an exciting opportunity for understanding the function and evolution of mirror neurons. Our understanding of these specialized neurons could be greatly advanced with comparative methods in behavioural neuroscience. With around 10,000 living species, birds are one of the most species-rich and diverse class of tetrapod vertebrate on the planet. Some communicate visually, some vocally and some both; some clearly learn their social behaviours, while others appear to guide interactions
with an innate repertoire of emotional reactions. Whether the behaviour is described as learned or innate however, both types of social behaviour (as well as their underlying neural substrates) appear to develop through the subject’s interactions with their social environment (e.g. Gilbertson 1975; Taziaux et al. 2007, King et al. 2005). In such cases, the mirror problem is a computational puzzle which must be solved to enable social development. Investigating the presence or absence of mirror neurons across bird species could help shed light on the degree to which these specialized neurons are necessary for social learning, and how their form and function varies between communicatively diverse species. The pigeon predominantly communicates visually, and, with the wealth of scientific reference material for supporting behavioural neuroscience in this species, the pigeon’s brain may be a good place to begin investigating the existence and function of mirror neurons in a visually communicating animal. Since the study of mirror neurons began, a broader view of the subject’s connection with its social environment has emerged and this has led to some unexpected developments. We should keep an open mind about where it might take us next.

4.3 Concluding remarks

This thesis aimed to provide a basis for further developing the pigeon as an animal model with which to investigate the mechanisms underlying interactive behavior in the visual communication channel. Until a few years ago there was only one articulated concept for explaining interactive social behaviour: if the only difference between two experimental conditions is the presence or absence of social contingency, then, animals or humans responding differently to these conditions must be capable of detecting social contingency (Watson 1966; Watson 1985; Gergely 2000; Watson 2001; Bigelow and DeCoste 2003; Hains and Muir 1996). Recently, however, a group of computational biologists, Auvray (2009) DiPaolo (2008; 2010) and Froese (2008; 2010) showed conclusively that social dynamics, in and of themselves, can
constitute processes underlying interactive behavior, in the absence of any individual psychology for evaluating the relations between social signals. The outcome was a new main explanation for interactive behaviour: perceptual crossing, where perceptual activities of the same nature interact with each other, resulting in dynamics that are fundamentally sensitive to the coherent structures of communication that they create.

4.3.1 The primary contributions of this work

To the author’s knowledge the work presented in this thesis is the first to investigate the role of perceptual crossing dynamics in a natural social interaction. This is perhaps the most unique and meaningful contribution of this thesis work. In contrast to the work of Auvray, DiPaolo and Froese, the present work is not a simulation nor a ‘minimalistic system’, but rather investigates a natural system – the circle walking interaction of pigeons – in which perceptual crossing dynamics are clearly acting to produce interactive behaviour in courtship. By studying these processes in a natural system, we have discovered that such dynamics are context specific (specific to courtship), we have also seen a glimpse of how perceptual crossing dynamics might interact with the animal’s individual (psychological) sensitivity to the signal response dynamic. To fully understand the interplay between social dynamics and interactive psychology that together make up the ‘interactive code’ of animal communication, the natural yet relatively simple system of pigeon courtship interaction is an ideal model for study. The findings stress the value of considering several alternative explanations for interactive social behaviour. In addition, while video playback researchers have always suspected potential experimental confounds arising from using inherently non-responsive video stimuli; we have conclusively demonstrated that, yes, the problem of confounds resulting from the absence of social interactivity in video playback research is real, and furthermore may be quite detrimental to the validity of both past and present work.
In discovering the role that perceptual crossing dynamics play in pigeon courtship, a potential third mechanism for interactive behaviour has been introduced here: IMI. Since perceptual crossing events, like eye contact, mutual touch and, in the pigeon, simultaneous circle walking, can predict meaningful fitness-related social outcomes, the evolution of mechanisms designed to sense perceptual crossing dynamics is a logical possibility. IMI is conceived to integrate the sensory experiences of perceptual crossing and reciprocal responsiveness to provide the individual with a general sense of mutual attunement. This mechanism might explain a number of phenomena where individuals appear to evaluate the coherence of social dynamics, but do not necessarily process signal relations in a way that utilizes the information about signal-response causation. In birds, for instance, the evolution of visual and vocal duetting would require an interactive perceptual integration process that functions to evaluate the quality of social interaction. The ritualized mutual displays in birds bear a striking similarity to the widespread human cross-cultural rituals of couples dance and song. In both animal and human duets, it is the ‘harmony’ within the couple’s interaction that is the main focus of the performance. Almost certainly, meaningful interactive signals do exist in subtle forms as well, such as in human interactional synchrony. In such cases, the subtlety might reflect the signal’s cooperative function and the benefit of sharing this social information at low costs to both individuals involved (see p.15). The pigeon and its simultaneous circle walking dynamics potentially present a unique opportunity to discover and study the neural basis of interactive multimodal integration.

4.3.2 Future directions

With the recent progress in the study of interactive behaviour, scientists observing social contingency sensitivity in behaviour may now have three mechanisms to consider, instead of just one: social dynamics, interactive multisensory integration and social feedback processing. These mechanisms are conceived to occur in evolutionary, developmental and functional ‘layers’;
interactive social dynamics provides a basis for IMI, and IMI provides a basis for social feedback processing. We believe the pigeon model can help scientists discover the mechanisms, structure and functions underlying interactive visual communication behaviour. The next three sections suggest some ideas for using pigeons to study perceptual crossing dynamics, IMI and social feedback processing.

4.3.2.1 Perceptual Crossing dynamics

It is possible that there is nothing going on in the pigeon’s brain alone to create interactive circle walking behaviour in courtship. They might be more similar to Walter’s robots, Elmer and Elsie, who seemed to coordinate their behaviour interactively with only a few ‘neurons’ controlling their actions (Walter 1950). Of course, the brain mechanisms involved, simple sensory-motor release, are integral in the interactive ‘system dynamic’ that emerges between them. But, with Elmer and Elsie and with potentially many social phenomena, only when the dynamic system of social interaction as a whole is considered, can one explain the emergence of their interactive behaviour. Elmer and Elsie’s interactive behaviour is driven by a perceptual crossing dynamic; but, each robot’s wiring, on its own, is not interactive and is not sensitive to inter-signal relations.

If perceptual crossing dynamics turn out to wholly describe interactive behaviour in pigeons, there are still many interesting questions about these dynamics that may be addressed using the pigeon model. For instance, how might the relative timing, spacing and relational qualities of perceptual crossing events influence their outcome? Could such factors create variations in the ‘intensity’ of perceptual crossing? We may have observed such an effect in male pigeons, where 3s time delays possibly potentiated circle walking by increasing the intensity of the perceptual crossing dynamic. Another question is: how do inter-individual and intra-individual variations in social display affect a pair’s social coherence? Are there certain
‘personalities’ (Schuett et al. 2009) of circle walking behavior and do certain combinations yield greater dynamic stability than others? For instance, do some individuals favour leftwards circle walking while other individuals favour rightwards circle walking, and, how would their combination affect the coherence of social dynamics? What influence does the dynamic form of the circle walk and its signaling components have on the stability of interactive courtship dynamics? How would the manipulation of physical abilities like injuries or movement constraints, environmental factors like barriers, restricted spaces and physical distance, social factors like conspecific audience members, or multisensory factors like vocalizations affect interactive behaviour and the social dynamic? How would the influence of sexual attractiveness on circle walking display interact with the effects of social contingency manipulations? Is the dynamic quality of courtship predictive of pair bonding, reproductive synchrony and mating success? Do pair members converge in circle walking patterns to become more congruent with one another over time? Could there be a greater diversity in meaningful social relations than those which are currently encompassed by the current definitions of perceptual crossing and signal-response relations?

Investigating such questions would help generate a general appreciation for factors that impact social dynamics and the effect they can have on social behavior and social outcomes. Social dynamics in humans have traditionally been studied using either greatly simplified, unnatural models of inter-individual coordination or highly complex models, like conversation (Haken et al. 1985; Schöner et al. 1986; Gilbert 1990; Prinz 1990; Schmidt et al. 1990; Bernieri et al. 1994; Schmidt et al. 1994; Schmidt and Turvey 1994; Oullier et al. 2005; Richardson et al. 2007; Macrae et al. 2008; van Ulzen et al. 2008; Miles et al. 2009). Highly simplified artificial interactions, like those between two peoples’ finger movements (e.g. Oullier et al. 2005), are removed from most of the social factors from which coordination dynamics may derive meaning. However, studying minimalist systems has the advantage of producing easily quantifiable data.
that can be represented in terms of the phasic relations between uniform rhythmic motions. Complex social interactions, like human conversation, cannot always be easily, or accurately, represented in this manner. An animal model, like the pigeon, has visual communication dynamics which are not overly simple but also not unmanageably complex and therefore might be an ideal system in which to study visual communication dynamics.

### 4.3.2.2 Interactive multisensory integration

In humans, there is much behavioural evidence for a ‘superficial sense’ of social dynamics. People in highly coordinated conversations express feelings of togetherness and rapport (Miles et al. 2009). It has been speculated that the reason music is so attractive and sought after is because it engages the listener in ritualized interactive social dynamics that exaggerate the meaningful dynamics of human interaction (Hagen and Bryant 2003; Fitch 2006). Is the sense of social dynamics unique to the human condition, or do other animals experience it as well? For instance, does the pigeon have a sense of coherence during SCW interaction, similar to what humans experience during well-coordinated conversation? The existence of duetting strongly implies that birds do perceive the coherence of social dynamics, and use this sense to evaluate the strength of their pair bond or the coalition quality of a neighboring pair (Wickler 1980; Hall 2000; Grafe and Bitz 2003; Hall 2005; Marshall-Ball et al. 2006). Also, just as humans exhibit spontaneous movement to rhythms in music, some animal species also engage with *human* music by coordinating their movements with the intensity and rhythm of the song (Patel et al. 2009; Schachner et al. 2009). Conceivably, these behaviours reflect an inherent sensory preference for engaging in perceptual crossing dynamics and participating in the multisensory stimulation patterns that are characteristic of natural social interaction.

**IMI is a highly attractive mechanism for its potential generality and simplicity.** An avian model in which to study IMI in the visual domain may help reveal why visual communication, in
particular, lends itself to a social sensation that, in humans, is reported as ‘feelings’ of social togetherness and rapport (Grammer et al. 1998; Lakin et al. 2003; Magnusson 2005). Perhaps perceptual crossing occurs primarily in the visual domain, since visual signals can occur simultaneously without interfering with signal transmission (see p. 11). This could help explain a number of phenomena: the human sense of social rapport from visual interactions alone (Grammer et al. 1998; 1990; 2000), the role that visual interactions appear to have in song learning (e.g. West and King 1988) and in maintaining the dynamics of duets (e.g. Williams 2001; Todt and Fiebelkorn 1980).

Whether or not the pigeon possesses IMI mechanisms would be a most interesting next step to pursue. Investigating whether SCW enhances behavioural circle walking responses by way of IMI requires separating these processes from the dynamical mechanisms that perceptual crossing entails. One method might be to strip the pigeon circle walking stimulus of all its pigeon qualities in order to artificially create, control and manipulate SCW dynamics, similar to the way that Wosegien’s (1989) used the human fist as a ‘social’ stimulus to show that head nodding appeases male aggression. IMI could also be investigated with stimuli that appear more natural, using either interactive video playback (Ord and Evans 2002; Toda and Watanabe 2008), or an interactive ‘virtual’ (animated) pigeon (Kunzler and Bakker 2001; Watanabe and Troje 2006; Van Dyk and Evans 2008). Such behavioural experiments could be useful; however, the question of whether IMI mechanisms exist or not would be most conclusively answered by searching for cells in the brain that integrate the multisensory cues of social interaction.

IMI mechanisms, if present, should be detectable at the cellular level (Barlow 1972). A study investigating the existence of brain cells exhibiting IMI properties during natural courtship interactions would require electrophysiological recordings from awake, circle walking subjects. Fortunately such methods are currently available (Vyssotski et al. 2006; Xiaofeng et al. 2009) and their use in songbird research has enabled an unprecedented ability to observe brain function
while the subject is actively engaged in social interaction (Kao et al. 2008; Prather et al. 2008). The candidate brain areas for containing cells with IMI properties include the lateral striatum, an area of the basal ganglia, which has already shown some preliminary evidence for IMI (Åkerman 1965) (see, p.142). In addition, visual association areas, especially NIL and mN, which integrate the visual features of social stimuli with other multisensory information, as well as motivation areas like pOA, would be obvious brain regions in which to search for the presence of IMI in the neuronal responses associated with pigeon courtship interactions.

4.3.2.3 Social feedback processing

It is possible that the pigeon brain acts as a controller in a closed-loop system defining social interaction, as described by Wolpert (2003). The wash of neuromodulatory action arising from ‘motivation’ areas of the brain could act to coordinate neural activity and plasticity between the brain regions controlling behaviour and the brain regions for perceiving conspecific signals (e.g. Alger, 2009). The result would be in reinforcing the behavioural and perceptual networks leading to favorable social outcomes and discarding those that do not, as occurs in socially reinforced operant learning (Gilbertson 1975).

If the pigeon does use social feedback mechanisms to shape social behaviour, it could be developed as a model in which to study clinical depression and anxiety syndromes that arise from unhealthy response patterns during social development (Watson, 2001; Gergely, 2000). Modeling social abuse and neglect could be achieved by manipulating the social contingencies described in the female signaling hypothesis (Patricelli 2006). For example, if a female pigeon head nods to reduce male courtship aggression and the male continues courting aggressively, thereby elevating the female’s fear and anxiety, the female might develop a pattern of learned helplessness that mimics abuse syndromes. Similarly if a pigeon learns that he or she cannot influence the circle
walking behaviour of their social partner, the animal might develop a pattern of learned helplessness that mimics syndromes arising from social neglect.

4.3.3 A final outlook

For the purpose of study, social interaction is almost always dissected into single individuals, and individuals are further dissected into separate psychological and behavioural processes. While this approach is valuable for testing specific hypotheses, it might be likened to the study of fish in experiments out of water. Social behaviour and social perception are fundamentally interlinked instruments that are shaped by their function together in a dynamic system of social interaction. By studying the whole system of communication, pigeon courtship behaviour has become understood as a fundamentally interactive process, which provides a basis for further developing the pigeon as interesting model in visual communication.

The songbird model has enabled an unprecedented level of empirical demonstration and insight into the inner-workings of vocal communication, and arguably, goes unmatched by any existing model in social neuroscience. This is largely due to the fact that the avian brain regions underlying social behaviour exhibit features like adult plasticity (Goldman and Nottebohm 1983; Marler and Nelson 1993) and sexual dimorphism (Balthazart and Ball 1995) that greatly afford and facilitate behavioural neuroscience (Shimizu et al. 2010). In the study of visual communication, the pigeon model, like the songbird, has the potential to also become an invaluable source of insight. The pigeon has a complex socio-sexual ecology which has many similarities to that of our own species, where performance in social competition and monogamous pair bonding come to define each individual’s reproductive fitness. Also, the rich scientific knowledge about the brain and behaviour of this species provides an important foundation for supporting its use in behavioural neuroscience.
Research investigating social interactivity in visual communication could not only help generate a basic understanding of social interaction, but could also achieve progress in many applied fields as well. From work in humans, we know that the presence of social contingency and coherence in visual communication can be influential in many everyday psychological processes, such as in forming social impressions, building friendships, optimizing business alliances, sustaining healthy marriages and so on (Maddux et al. 2008; Grammer 2000; Tickle-Degnen et al. 1990; Bernieri et al. 1988; Sharpley et al. 2001; Miles et al. 2009; Lakin, 2003). The work in animal species suggests a similar set of functions, coordinating courtship, communicating mutual attraction, mediating social preference, sustaining pair bonds and achieving efficient communication (Hall 2003; Royle and Pike 2010; Trainor, 2000). Unhealthy social dynamics underlie several serious social pathologies. Therefore attention to the mechanisms underlying interactive social behaviour, which may constitute a distinct, previously underappreciated feature of these problems, has a potential for great clinical significance. The benefit of understanding these processes would be in understanding how to intervene and stop unhealthy dynamics from ‘snowballing’ catastrophically or how to promote dynamics which nurture learning, bonding and other positive outcomes. If the mechanisms underlying interactive behaviour are psychological, pathology in a patient’s perceptual or cognitive processing of social contingencies might be modifiable through a combination of behavioural, cognitive and pharmacological treatments. Key to developing such treatments would be an understanding of the neural processes underlying the psychology underlying interactive behaviour, the attainment of which requires the type of behavioural neuroscience that is only attainable in animal research.

In addition to its clinical applications, research towards understanding the interactive processes of visual communication has applications ranging from developing user-friendly interactive interfaces to understanding and controlling the social processes that underlie conflict and cooperation. Interactive social mechanisms are fundamental, and knowledge about their unique
form in the visual aspects of communication could potentially shed light on so many interesting human experiences. From bullying to negotiating to peacemaking, virtually, any human phenomena involving social interaction might benefit from this approach.
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