SOCIAL COGNITION IN DOMESTIC HORSES

(*EQUUS CABALLUS*)

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Doctor of Philosophy

Leanne Proops

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I herby declare that this thesis has not been and will not be, submitted in whole or in part to another University for the award of any other degree.

Signature……………………………………………………………………………

Leanne Proops

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SUMMARY

The social intelligence hypothesis states that the main selection pressures driving increases in brain-to-body ratio are social rather than ecological. The domestic horse is an ideal animal to study within this framework because horses possess rich social lives but inhabit simple ecological environments. Here I assess the abilities of horses within two broad areas of social cognition; the classification of, and the use of information obtained from, social partners. In Section One I demonstrate that horses are capable of cross-modal individual recognition of conspecifics, an ability not previously demonstrated conclusively outside of humans. This ability extends to identifying familiar human companions suggesting that recognition systems are highly plastic in the individuals they can encode. These results also provide the first insights into the brain mechanisms involved in this process by revealing a clear left hemisphere bias in discriminatory ability. In Section Two I investigate the extent to which horses are capable of reading human attentional and communicative cues. It has been suggested that this skill was selected for through the process of domestication, however there have been no systematic studies of domestic animals other than the domestic dog. I found that horses were indeed highly skilled at determining if people were paying attention to them. In contrast they tended to only use basic stimulus enhancement cues to choose a rewarded bucket. A further study of young horses indicated that the ability to detect human attention requires significant experience to develop fully whereas the ability to use stimulus enhancement cues in an object choice task appears to require far less (if any) experience to develop. Overall my thesis extends our knowledge of comparative social cognition and in particular our knowledge of social cognition in horses. Taken together, these results clearly demonstrate that horses do indeed possess some complex socio-cognitive skills.

CO-AUTHORSHIP STATEMENT

I am the principal author on all the manuscripts that comprise this thesis and have been in charge of all aspects of the design, implementation, analysis and dissemination of this research. My supervisor Dr Karen McComb is included as a co-author on all manuscripts as her expertise and advice have been invaluable throughout all stages of my work from the initial planning of experiments through to the final preparation of research papers. My second supervisor, Dr David Reby is included as a co-author for Article I as he made important contributions to the design of the study and provided useful comments during the drafting of this manuscript. Megan Walton is included as a co-author for Article IV in recognition of her significant contribution to data collection as part of her undergraduate project.

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INTRODUCTION

"There are still many unanswered questions, and future research on animal social cognition should… attempt to establish the full range of social-cognitive skills for a wide range of animal species. It also remains to be determined what role individuals' social experiences (including with humans, when appropriate) play in the development of sensitivity to the attentional states of others and in social-cognitive development in general."

Call, Bräuer, Kaminski and Tomasello (2003) p263.

SOCIAL BRAINS AND SOCIAL COGNITION

Social brain hypothesis

Since Darwin first proposed his theory of evolution by natural selection, scientists have tended to think of the cognitive abilities of animals as having been adapted to fit their particular ecological niche rather than their social environment. Correspondingly, evolutionary leaps in brain size within primates and specifically hominids were generally attributed to natural selection favouring individuals able to succeed in increasingly complex ecological environments (Clutton-Brock and Harvey 1977; Emlen and Oring 1977). Increases in, for example, the complexity of the foraging techniques in primate species were found to correlate with higher brain to body ratios (Clutton-Brock and Harvey 1980). The behavioural plasticity of species and their ability to adjust to novel environments have also been seen as indicators of adaptation to environmentally complex niches (Sol et al. 2005).

However, another factor that often co-varies with ecological complexity within taxa (including primates, carnivores and birds) is social complexity (Shultz and Dunbar 2006). Thus an alternative hypothesis that is currently gaining much support is the social brain hypothesis, which states that in many taxa the main

selection pressure for larger brains is social rather than environmental (Jolly 1966; Humphrey 1976; Dunbar 1998). Those animals within a group that are more able to recognise conspecifics and read their communicative signals, to communicate clearly their intent and form alliances, will be more successful. This selection for social ability is believed to lead to increases in relative brain size as a result of the increased processing power required to orchestrate social relationships in large or complex social groups. A correlation between group size or complexity and relative brain size has been found not just in primates (in which specifically the size of the neocortex compared to the rest of the brain is a good predictor of social complexity) but also in other taxa such as the Cetacea, Carnivora and some Insectivora (Dunbar and Bever 1998; Marino 2002; Dunbar 2003).

Horses present a particularly useful model for exploring the evolution of social intelligence within this framework because unlike primates and cetaceans, and like many other ungulate species, they have a relatively simple foraging behaviour (ecological environment) but complex social organization and so the effects of the two can be more readily teased out and assessed. Recent work suggests that the social brain hypothesis can indeed be applied to ungulates (Perez-Barberia and Gordon 2005). Comparative analysis of ungulate species has revealed that evolutionary increases in brain size over time are correlated with increases in sociality (Perez-Barberia et al. 2007). In addition, Perissodactyls (odd-toed ungulates), the order to which horses belong, have seen considerable encephalisation over time, with only primates and cetaceans undergoing greater increases. Specifically, the suborder of hippomorpha that contains only one extant family, the Equidae, has undergone particularly large increases in encephalisation compared to other ungulates (Shultz and Dunbar 2010). Neocortex size in ungulates is predicted not by habitat use or by overall group size but by the complexity of the group, thus species living primarily in smaller cohesive groups, such as horses, have larger relative neocortex size than species living in large unbonded aggregations (Shultz and Dunbar 2006).

It is therefore likely that any "advanced" cognitive adaptations horses possess have been driven by social demands and one may indeed expect to find complex social skills within this group.

What is social cognition?

Social cognition has been defined as "cognitive processes that operate on information derived from, or relevant to, other animals" (Rooney and Bradshaw 2006). The study of social cognition encompasses a wide variety of research fields including those concerning the categorization of social partners and their emotions, the use of information obtained from social partners, the development and management of social relationships, the role of social learning, the manipulation of others through communication, the engagement in joint cooperative actions and the question of whether animals possess an understanding of the mental life of others (Miklosi et al. 2004).

In this thesis I investigate the socio-cognitive skills of horses within two broad fields of social cognition: the discrimination and categorisation of social partners and the use of information obtained from social partners. In the following introductory sections I outline the relevant research conducted in these fields and the methods employed to gain insights into these abilities. I also highlight the current controversies and unanswered questions within these areas.

Discrimination and classification of social partners

Introduction

The ways animals classify others reflects the selective pressures placed on them and provides insights into the social structure of a species and how they perceive the world (Cheney and Seyfarth 1982). Discrimination of kin from non-kin, as well as individuals within both of these categories, has been proposed to be of major significance in the evolution of social behaviour (Hamilton 1963; Trivers 1974). The extent to which these abilities are present in a species will

reflect the extent to which being recognised by conspecifics represents an adaptive advantage. Individual recognition is the most fine-grained categorisation of social partners and may be more important for species that live in fluid fission-fusion societies and form social groups that are not primarily familial, such as horses. The classification of individuals within such societies may be more graded and complex than a simple distinction between ingroup and outgoup members (Aureli et al. 2008). Being able to recognise individuals and remember their specific attributes, such as dominance, gender, kinship and degree of association is an important basis for more complex social cognition such as forming alliances (Pennisi 2006). However, there is still much controversy and debate surrounding what constitutes sound evidence of individual recognition.

Discrimination between basic features of individuals such as sex or age would allow an animal to classify individuals as belonging to a certain group (e.g. male or female) without necessarily having interacted with them before. Apparent recognition of a neighbour, for example, may merely involve discrimination between familiar and unfamiliar cues that depend on a context specific association between a location and an acoustic or visual signal (Rendall et al. 1996). Thus a neighbour may be identified as familiar if he is heard in his familiar territory but not if he is heard in a different location (Husak and Fox 2003). Recognition of a specific individual goes beyond this and not only requires that identity cues are discriminated at the level of the individual rather than a broader category, but also that these cues match stored information about that specific individual. In other words an animal must not only know that identity cue A is different from identity cue B but that identity cue A belongs to animal A and identity cue B belongs to animal B. Some researchers also consider both neighbour-stranger and parent-offspring discrimination a more basic process than genuine individual recognition because it does not require the recognition and categorisation of a large number of known individuals (Rendall et al. 1996; Tibbetts and Dale 2007).

The precise definition of what constitutes evidence of individual recognition remains highly controversial. What I present here is the most stringent and

rigorous definition. Some researchers believe this form of definition is too narrow and that when animals learn specific characteristics of an individual in order to classify them into a broad category such as "neighbour", "offspring", "mate" or "dominant" (thus using a memory of this individual rather than some form of universal signal of that class), this should also be considered individual recognition (Steiger and Muller 2008). I, however, believe that it is vital that evidence for individual recognition demonstrates that the representation of the individual contains unique information corresponding to that particular individual. This is clearly what is meant by individual recognition when referring to the process in humans. Many others believe that if the identity cue can be shown to retrieve information about that individual, such as their specific rank, and hence produce a seemingly unique response to that individual this could similarly be considered individual recognition (Tibbetts and Dale 2007; Tibbetts et al. 2008). The problem with this definition is that truly unique responses are difficult to define and, for example, an amodal discrimination of a dominant versus subordinate individual may reflect information encoded within the broad categories of higher and lower rank. Furthermore an important feature of individual recognition in humans is that it is cross-modal. It is thus crucial to determine whether individual recognition can be independent of modality in other animals.

The following section details how behavioural studies have furthered our understanding of how animals discriminate and categorise social partners in the visual, vocal and cross-modal domains. The focus will be on attempts to demonstrate complex and fine-grained discrimination of others. I then go on to consider the possible neural bases of these skills.

Vocal discrimination and classification of social partners

There is considerable evidence that a number of species are able to make important distinctions between categories of individuals on the basis of their acoustic calls, and on the basis of these calls, retrieve additional information about the caller (such as affiliation) to be used in deciding how to react (Seyfarth and Cheney 2003). Distinct individual vocal characteristics have been

found for a number of different taxa including some primates, marine mammals, ungulates, canids and birds (for a review see Yin and McCowan 2004; Reby et al. 2006; Taylor and Reby 2010). In general, animals that live in large groups have more individually distinct vocalisations than individuals that live in small groups (Pollard and Blumstein 2011).

For a call or call feature to convey individual identity it must have high inter-individual variation and low intra-individual variation. Some calls within a species' vocal repertoire are better suited to individual recognition than others, for example the function of contact calls suggests they are likely to have evolved to carry individual signatures and both tonal and broadband qualities may serve to facilitate this (Kondo and Watanabe 2009). In contrast, alarm calls are often more noisy and may be adapted to be highly stereotyped across individuals so they are easily understood. Agonistic vocalisations given during male-male competition are again often harsh, presumably to emphasize acoustic characteristics that advertise body size (e.g. fallow deer (*Dama dama*); Vannoni and McElligott 2007). However, individual identity is not just encoded in contacts calls and can extend to other call types, such as the alarm calls of some primates and rodents (for reviews see Pollard 2011; Zuberbuehler 2009). In mixed-species flocks of birds, where indivduals are unlikely to interact repeatedly, deceptive alarm calling has been reported and it has been suggested that the function of encoding identity in alarm calls may be to allow receivers to assess the reliability of the caller (Munn 1986; Sproul et al 2006; Zuberbuehler 2009). This may also facilitate the recruitment of help and the distictiveness of alarm calls has been found to be higher in social *Marmotinae* species (in which groups consist of related individuals), than less social species (Matrosova et al. 2011). Since the species in which individualistic alarm calls have been reported tend to form social groups of related individuals, it is difficult to separate these two potential (and not mutually exclusive) functions of individualistic alarm calls - to determine the reliability of the caller and as a mechanism of kin selection. In addition, there is also evidence that some species possess unique vocal signatures that are stable across multiple call types, these are likely to reflect the physiological properties of the individual and are akin to the individual voice of humans (e.g. rhesus macaques (*Macaca*

mulatta), Rendall et al. 1998; African elephants (*Loxodonta africana*), Clemins et al. 2005; red deer (*Cervus elaphus*), Reby et al. 2006; fallow deer, Vannoni and McElligott 2007).

A wide variety of species discriminate between the calls of familiar and unfamiliar conspecifics and preferentially respond or respond positively to familiar callers (e.g. red deer; Reby et al. 2001; wolves (*Canis lupus*) and Arctic foxes (*Vulpes lagopus*); Frommolt et al. 2003; cottontop tamarins; Jordan et al. 2004; chimpanzees (*Pan troglodytes*); Herbinger et al. 2009; horses; Lemasson et al. 2009). Playbacks of calls to individual African elephants showed that they discriminate between calls of close associates and distant associates. A conservative estimate of the number of callers an individual elephant was familiar with was around 100 adults, suggesting elephants have a considerable capacity for remembering the calls of conspecifics (McComb et al. 2000). In elephant societies, as with many Old World monkeys and cetaceans, stable matrilineal groups exist and are led by an older matriarch. It was found that among African elephants, older matriarchs were more skilled at discriminating between calls differing in levels of familiarity and that the families led by an older matriarch also had higher reproductive success, highlighting the importance of fine-grained discrimination between conspecifics in social species (McComb et al. 2001).

The habituation-dishabituation paradigm is widely used to assess how animals discriminate between the identity cues of different individuals. In vocal communication studies, if a subject habituates to the calls of one signaller then dishabituates to a call given by a different signaller, this indicates that the animal perceives the call to be different from the previous ones in some way. This method has been used to show, for example, that rhesus macaques can discriminate between the calls of different familiar matrilineal kin (Rendall et al. 1996). This paradigm does not, however, make it clear whether actual identity is assigned to the calls or whether discrimination was made on the basis of very fine differences in familiarity. It is possible that the macaques were habituating to the acoustic properties of the different calls that reflect the anatomy and physiology of the individual and are therefore stable across vocalisations from

individual callers. One such acoustic property is formant structure, an attribute rhesus macaques are known to perceive (Ghazanfar et al. 2007). This discrimination would not involve assigning identity to the calls, or even necessarily being familiar with the signaller prior to the presentation of the calls. Red deer and pandas for example, have been shown to dishabituate to changes in callers when presented with vocalisations from unknown individuals (Charlton et al. 2007; Charlton et al. 2009). As such, these results are compelling but do not require individual vocal recognition, simply the discrimination of different acoustic stimuli.

The long-term study of baboons (*Papio cynocephalus ursinus*) conducted by Cheney and Seyfarth has led to a detailed understanding of how individuals from this species are able to classify one another, with corresponding insights into the perceptual world of these primates. As has been mentioned previously, many Old World monkeys are able to discriminate between the calls of others based on individual identity, the rank of the caller and also the matrilineal group to which they belong. Recent work suggests that these features of a caller can be retrieved simultaneously, for example, anomalous rank interactions, where a lower ranking individual is heard threatening a higher ranking individual, are not only distinguished from accepted rank interactions but the receiver also discriminates between within-family rank reversals and between-family rank reversals (Bergman et al. 2003; Seyfarth et al. 2005). Thus the call of a conspecific appears to elicit the retrieval of complex and hierarchically arranged knowledge about the caller such as rank, matriline and troop membership. However, in these studies, only auditory information is presented. Without the chance for the receivers to match this information to specific individuals visually, the possibility that the signaller's vocalisation is being paired with information from a broader class than just the individual, such as higher versus lower rank, cannot be conclusively excluded.

Perhaps the most individually distinct of all animal calls is the dolphin (*Tursiops aduncus*) signature whistle. Within their vocal repertoire each dolphin appears to have a call that has a unique temporal pattern and is used as a cohesion call when individuals are separated from other group members (Janik and Slater

1998; Janik et al. 2006). Group members reply to the signature whistles of isolated individuals either by giving their own signature whistle or that of the isolated individual (Janik and Slater 1998; Janik 2000). In terrestrial mammals, individual identity often appears to be encoded in the caller's voice features rather than the temporal pattern – however in water these acoustic features may attenuate quickly so temporal parameters are likely to be more salient. Additionally, unlike many other mammal species where individual distinctiveness appears to be a by-product of physical characteristics and thereby essentially a passive process, conveying individual information via pitch contour appears to require learning. Dolphins have been found to learn a signature whistle of a rarely encountered individual and modify it slightly to produce their own unique call (Janik 2000). Simple temporal characteristics of elephant seal (*Mirounga leonina)* calls are also believed to be learnt through imitation (Sanvito et al. 2007). The unusual form of dolphin signature whistles, coupled with the fact that members use the signature whistle of associates during interactions suggests that signature whistles may be functionally similar to human names (Barton 2006; Janik et al. 2006). A conclusive demonstration of the referential nature of signature whistles would be provided if dolphins were shown to spontaneously produce the signature whistle of an individual visually presented to them.

The vocalisations of heterospecifics may also be highly salient to some species and the use of heterospecific alarm calls by certain reptiles, birds and mammals is well documented (for a review see Kitchen et al. 2010). For some animals, particularly domestic animals, it is adaptive to understand communication from humans, however, there have been very few studies into this area and none to my knowledge looks at how animals classify people into social groups and potentially discriminate between individuals based on their voices alone. One study found that dogs (*Canis familiaris*) performed better when their handler was heard issuing a command compared to a stranger, suggesting that there was some degree of discrimination between the voice of the familiar handler and an unknown person (Coutellier 2006).

Visual discrimination and classification of social partners

Individual recognition has been suggested as an important but poorly understood factor driving the evolution and maintenance of phenotypic diversity (Tibbetts and Dale 2007). As with vocal communication, a large number of species have been shown to categorise others on the basis of visual appearance. Discrimination between broad categories of individuals may involve phenotypic matching of signals that reflect that particular class such as the discrimination of related individuals or the discrimination between dominant and subordinate individuals via status signalling or winner-loser effects (Ligout and Porter 2006). The more complex discrimination between familiar and unfamiliar individuals and the recognition of particular individuals requires the encoding of specific traits with high inter-individual variability and low intra-individual variability. What remains unclear is whether the phenotypic traits of particular individuals are stored as precise multi-modal representations of these individuals or whether, when seen, these individuals activate more general concepts such as "dominant" or "familiar".

Visual discrimination of familiar versus unfamiliar unrelated individuals, such as neighbours or mates is commonplace and has been documented in insects (Muller et al. 2003), lizards (Husak and Fox 2003), fish (Waas and Colgan 1994), invertebrates (Detto et al. 2006), birds (Whitfield 1986), terrestrial and marine mammals (Amos et al. 1995; McLeman et al. 2008). In this case individual phenotypic traits may be learnt but, as noted before, positional information rather than individual recognition may underlie some forms of mate and neighbour discrimination. For example, burying beetles (*Nicrophorus vespilloides*) are considered mates if they have been at the nest site for several days (Muller et al. 2003). The sight of individuals can produce reactions by conspecifics that suggest that they have attached other attributes to the individual seen, such as whether they are trustworthy neighbours (red wing blackbirds (*Agelaius phoeniceus*); Olendorf et al. 2004), cooperative partners (guppies (*Poecilia reticulata*); Dugatkin and Alfieri 1991) or the most useful potential collaborators (chimpanzees; Melis et al. 2006). Rank or relative dominance of a conspecific previously battled, or observed in combat, can also

be determined upon their return by some insects (Tibbetts 2002), invertebrates (Gherardi et al. 2010) fish (Grosenick et al. 2007), birds (Bond et al. 2003) and mammals (Silk 1999; de Villiers et al. 2003). Again it is difficult to determine how precise the representations of these individuals are, in particular whether they are assigned to broad categories such as rank or familiarity or whether genuine individual recognition is occurring. It should also be noted that in many of these naturalistic studies additional olfactory cues might have contributed to the discrimination.

One way to determine if animals are capable of discriminating and classifying individuals on the basis of their appearance is by using a matching-to-sample paradigm. Here animals are trained – and this generally requires extensive training - to match the image of one individual or class of individuals, with another image of the same individual or class. Often they are then presented with new exemplars to see if the animal has formed a general rule of categorisation. This method shows that an animal has the potential to make the particular discrimination and has been used, for example, to demonstrate that primates have a concept of "mother-offspring" or "dominant-subordinate" (Dasser 1988; Bovet and Washburn 2003) and that pigeons (*Columba livia*) can form the concept "familiar" (Wilkinson et al. 2010a). This technique can also be used to demonstrate that subjects are able to discriminate between individuals when shown photographs of these individuals taken from different perspectives (Nakamura et al. 2003). One highly salient feature used by humans for visual recognition of individuals is the face. Many primate species, cattle (*Bos Taurus*) and sheep (*Ovis aries*) can discriminate between familiar and unfamiliar conspecific faces and in matching to sample studies can extrapolate this familiarity rule to classify novel face pairings (Rosenfeld and Vanhoesen 1979; Dittrich 1994; Kendrick et al. 1996; Parr 2003; Ferreira et al. 2004; Coulon et al. 2009; Marechal et al. 2010; Coulon et al. 2011). In naturalistic tests, crayfish (*Cherax destructor*) discriminate between the faces of previous opponents and paper wasps (*Polistes fuscatus*) discriminate individual nest mates (Tibbetts 2002; Van der Velden et al. 2008).

Again, for many animals, humans represent significant social partners (and sometimes a significant threat) so an ability to recognise familiar people and distinguish between friendly and unfriendly individuals would be advantageous. Some species of mammal, bird and marine invertebrate have been shown to learn to associate positive and negative/neutral interactions with two different humans (Davis et al. 1998; Taylor and Davis 1998; Davis and Gibson 2000; Davis and Taylor 2001; Koba and Tanida 2001; Anderson et al. 2010). Rats (*Rattus norvegicus*), seals and even cockroaches (*Gromphadorhina portentosa*) have been shown to habituate to specific handlers (Davis et al. 1997; Taylor et al. 1998; Davis and Heslop 2004). In spontaneous or more naturalistic tests of knowledge acquisition, elephants have been shown to discriminate between dangerous Masai tribesmen and individuals from other tribes on the basis of garment colour and odour (Bates et al. 2007). Mockingbirds (*Mimus polyglottos*) also learn very quickly to identify specific individuals that threaten their nests and respond more vigorously to these than to other individuals - and there is some evidence that this discrimination can be made on the basis of facial cues (Levey et al. 2009). When presented with only facial cues, sheep prefer to look at familiar versus unfamiliar people while cattle appear not to attend to these cues (Rybarczyk et al. 2001; Kendrick 2006). Crows (*Corvus brachyrhynchos*) have also been found to use facial features to identify humans that had previously trapped them (Marzluff et al. 2010). In a matching-to-sample task pigeons learnt to discriminate between photographs of the heads of different people but showed no sign of recognising them in person (Dittrich et al. 2010). In contrast, horses have been shown to transfer discrimination of individual human faces to the actual person (Stone 2009).

Cross-modal discrimination and classification of social partners

The ability to transfer information cross-modally was once thought to be unique to humans (Ettlinger 1967). However, recent research has shown a number of vertebrate species are capable of integrating multi-sensory information in a socially relevant way. Using a preferential looking paradigm, which exploits the tendency of animals to look at the congruent stimuli, rhesus macaques have been shown to spontaneously match the number of vocalisers heard to the

corresponding number of conspecifics presented visually (Jordan et al. 2005). They also match calls given by small or large conspecifics to the corresponding visual image and the sound of coo or threat calls to the video showing a conspecific emitting this type of call, although this task can be solved by matching signal onset and ending with mouth configuration (Ghazanfar and Logothetis 2003; Ghazanfar et al. 2007). Capuchins (*Cebus apella*) can also match the call type/vocalisation of rhesus macaques and humans to the correct image presented (Evans et al. 2005). When chimpanzees were presented with incongruent auditory and visual cues, the most salient cue to identification of calls depended on the call type (Parr 2004). Pant hoots and play faces were categorised on the basis of auditory cues whereas screams were categorised primarily on the basis of visual information. Thus different sensory modalities were preferred depending on the nature of the calls.

As noted previously, a key feature of human individual recognition is that it is cross-modal, thus voice and face can be matched, and stored information about that particular individual can be accessed via cues from multiple sensory modalities. In field studies, animals often produce apparent cross-modal reactions to stimuli suggesting they have matched the identity information to a specific individual. For example, given playbacks of the screams of juvenile vervet monkeys (*Cercopithecus aethiops*), adults will look towards the mother upon hearing the scream of her particular infant, demonstrating a cross-modal association between the calls and the sight of the corresponding mother (Cheney and Seyfarth 1980). Similarly, when subordinate baboons are played the reconciliatory grunts of a dominant that has just been aggressive to them, they are more likely to approach that specific individual and accept their approaches compared to other dominant individuals (Cheney and Seyfarth 1997). When a particular family member is walking behind them, elephants show surprise at encountering urine from that individual on the path in front of them, suggesting that they are aware that the position of an individual should correspond to the location of its olfactory cues (Bates et al. 2008). However, as stipulated earlier, without controlled studies we cannot be sure if cross-modal individual recognition is the mechanism by which such complex classification of social partners occurs.

In laboratory based studies, hamsters (*Mesocricetus auratus*) have been shown to associate multiple identity cues from one sensory modality, olfaction, to familiar individuals (Johnston and Peng 2008). The matching to sample technique has also shown that a few highly trained and enculturated chimpanzees are capable of matching various calls to pictures of individual conspecifics and in some cases, humans, after extensive periods of learning (Bauer and Philip 1983; Kojima et al. 2003; Izumi and Kojima 2004) and this ability has also been shown to transfer to new face-voice pairings (Martinez and Matsuzawa 2009). I use the term enculturated here to define a rearing environment where animals have a great deal of exposure to people, their artifacts and the human sociocultural environment; for apes this may include learning some form of language system (Furlong et al. 2008). The ability to learn the signature whistles of unknown individuals and associate them with different symbols has also been shown in a dolphin, who was then able to transfer her response to new recordings of signature whistles from the same individuals (Harley 2008).

The ability to spontaneously integrate cross-modal identity cues has also been demonstrated using an expectancy violation paradigm. Here the subjects are presented with the identity cues from one person in one sensory modality and then identity cues either from the same person or a different person in an alternative sensory modality. In this case, subjects will look for longer if the cues are incongruent compared to if they are congruent. The benefit of this and the preferential looking paradigm is that, unlike matching to sample tasks, they test for existing knowledge without the need for extensive training. In one study dogs were presented with the voice of either their handler or a stranger followed by the image of either person. Dogs showed surprise, i.e. looked for longer, when the face seen did not match the voice just heard (Adachi et al. 2007). In a similar study, squirrel monkeys (*Saimiri sciureus*) were trained to match to sample photographs of two handlers. In probe trials the voice of either the congruent or incongruent caretaker was played between the presentation of a sample stimulus and the choice stimuli. When the least familiar caretaker's photograph was presented and the most familiar caretaker's voice was heard,

the monkey's matching accuracy was significantly reduced but the sound of the least familiar caretaker's voice did not interfere with the subjects' ability to match the photographs of the most familiar caretaker (Adachi and Fujita 2007). Thus in both cases subjects appear to possess cross-modal representations of one highly familiar human caretaker. However, their discrimination was of only one familiar handler and because the presentation of cues to the familiar individual were paired with cues to either a much less familiar individual or a stranger, we cannot be sure how precise these representations are.

Neural bases of the discrimination and classification of social partners

The neural mechanisms involved in the ability to categorise social partners are now starting to be uncovered in humans, however far less is known about the neural bases of these skills in animals. Although the processing of language is strongly lateralised in the left hemisphere in humans, the processing of non-verbal information in speech, including the identity of the caller, tends to primarily activate areas of the superior temporal sulcus (STS) in the right hemisphere. A recent study has found areas in the superior temporal plane of the primate brain that respond to conspecific calls and are sensitive to the identity of conspecific callers, suggesting the presence of an area specialised in the identification of conspecific calls that is homologous to the area of the STS found in humans (Petkov et al. 2008). In humans specialised facial processing areas have been located in the in the fusiform gyrus and STS, particularly in the right hemisphere (for a review see Campanella and Belin 2007; Brancucci et al. 2009; Leopold and Rhodes 2010). Specific face-sensitive areas have also been located in the primate and sheep brain, with neurons being found that are activated by the sight of specific individual faces, suggesting that special face-sensitive cortical areas may be widespread among social mammals (Tate et al. 2006; Leopold and Rhodes 2010).

Far less is known about the mechanisms involved in the recognition of familiar individuals using multi-sensory integration of voice-face (or voice-body) information, with findings being largely based on studies determining areas that are activated similarly when subjects are presented with either visual or auditory

identity information. These results tend to suggest a synchronisation of activation between face selective and voice selective areas, often with activation of additional cortical areas that may be the location of semantic information about specific individuals, so called "person identity nodes" (for a review see Campanella and Belin 2007). Right hemispheric activation of face and voice selective areas and the hippocampus has been reported during recognition tasks (von Kriegstein and Giraud 2006; Joassin et al. 2009; Hertrich et al. 2011). Differences in the activity of multi-sensory cortical areas have also been reported when subjects are presented with congruent or incongruent face–voice pairs. Similar patterns of activation are seen in primates. When macaques either viewed footage of conspecifics producing vocalisations or heard the vocalisations themselves, activation was produced in the auditory cortex and higher-order visual areas, as well as multi-sensory areas of association cortex (Gil-Da-Costa et al. 2004; Sugihara et al. 2006; Ghazanfar et al. 2008). It has been suggested that the neocortex is essentially multi-sensory in nature and therefore some form of cross-modal processing is likely to be widespread across mammal taxa (Ghazanfar and Schroeder 2006).

While very few other studies of mammals outside of those conducted with primates and sheep have isolated specific cortical areas controlling the categorisation of others, a large number of behavioural and neurophysiological studies have shown general hemispheric specialisation in the processing of auditory and visual social stimuli across a wide variety of species. Several animal species appear to have a left hemisphere bias for the processing of conspecific vocalisations including Japanese macaques (*Macaca fuscata*) (Petersen et al. 1978; Heffner and Heffner 1984), rhesus macaques (Hauser and Andersson 1994; Poremba et al. 2004), Californian sea lions (*Zalophus californianus*) (Boye et al. 2005), domestic dogs (Siniscalchi et al. 2008), house mice (*Mus musculus*) (Ehret 1987), Harpy eagles (*Harpia harpyja*) (Palleroni and Hauser 2003) and male but not female mouse lemurs (*Microcebus murinus*) (Scheumann and Zimmermann 2008). However, other species demonstrate a right hemisphere bias (e.g. vervet monkeys; Gil-da-Costa and Hauser 2006) or fail to show lateralisation (e.g. Barbary macaques (*Macaca sylvanus)*; Teufel et al. 2007*).

In contrast heterospecific calls and non-biological sounds tend to either be processed by the right hemisphere (Hauser and Andersson 1994; Hauser et al. 1998; Ghazanfar et al. 2001; Poremba et al. 2004; Siniscalchi et al. 2008) or do not appear to be lateralised (Petersen et al. 1978; Hauser et al. 1998; Boye et al. 2005; Gil-da-Costa and Hauser 2006; Lemasson et al. 2010), suggesting that there is something unique about conspecific calls. Although some of the comparative heterospecific calls played to subjects in these studies were to some degree familiar (e.g. Hauser and Andersson 1994), the extent to which familiarity or salience may affect the way in which heterospecific acoustic stimuli are processed is not clear. Certainly some studies have shown that the level of familiarity with a conspecific call affects the pattern of lateralisation, with zebra finches (*Taeniopygia guttata*) (Cynx et al. 1992) and bonobos (*Pan paniscus*) showing a left hemisphere bias specifically for familiar conspecific calls (Taglialatela 2004). In Harpy eagles conspecific calls are processed in the left hemisphere, while the calls of non-prey species are processed in the right hemisphere. Meanwhile, the calls of prey species were found to be processed in the right hemisphere of naive individuals that had not hunted before but once eagles had hunting experience the calls became processed in the left hemisphere, suggesting it is not just exposure to a heterospecific vocalisation but its salience that may affect how the call is processed (Palleroni and Hauser 2003).

For domestic animals such as dogs and horses, human voices are both highly salient and very familiar, in some cases, being more familiar than conspecific calls. In addition there would be distinct selective advantages to being "tuned in" to human vocal communication that may have led to adaptations for processing this stimuli. To my knowledge no study has looked at hemispheric processing of natural human speech by domestic animals.

In the visual domain, conspecifics appear to be preferentially viewed with the left eye (right hemisphere) in a wide range of mammals (Sakai et al. 2006), birds (Vallortigara 1992), reptiles (Bisazza et al. 2002) and fish (Sovrano 2004). This preference is found across a variety of social situations including

aggressive encounters (Deckel 1995; Casperd and Dunbar 1996; Hews and Worthington 2001), sexual behaviour (Ventolini et al. 2005; Gulbetekin et al. 2007) and discrimination between familiar and unfamiliar conspecifics either via whole body or facial cues (Hamilton and Vermeire 1988; Vallortigara and Andrew 1994). Several studies have shown that the familiarity of the conspecific affects laterality with some species, such as sheep, showing a right hemisphere bias for the discrimination of familiar conspecifics and no strong lateralisation for unfamiliar conspecifics (Peirce et al. 2000), and quails showing (*Coturnix coturnix X Coturnix* japonica) a right hemisphere bias for familiar individuals and a left hemisphere bias for strangers (Zucca and Sovrano 2008).

The viewing of heterospecifics has also been shown to be governed by the right hemisphere in most species tested (Evans et al. 1993; Cantalupo et al. 1995; Lippolis et al. 2005). However, the mechanisms involved are likely to be different, with responses to heterospecifics being governed by pathways associated with predator avoidance. This finding supports the theory that the right hemisphere controls fear responses and processes negative emotions whereas the left hemisphere governs approach behaviour (MacNeilage et al. 2009; Rogers 2010). However, differential processing of visual cues from familiar and unfamiliar conspecifics suggests that familiarity with a heterospecific may also alter the way in which their individual identity is processed. Chickens (*Gallus gallus*) with no experience of humans (and as such probably view humans as predators) showed a left eye preference for viewing an image of a human face, whereas no lateralisation was seen in subjects that were familiar with humans (Daisley et al. 2009). In contrast, highly enculturated dolphins show a weak right hemisphere preference for viewing both familiar and unfamiliar people (Thieltges et al. 2011) and sheep show a right hemisphere bias for familiar sheep but show no lateralisation for discriminating between the faces of highly familiar human handlers suggesting that they don't use the same mechanisms for discriminating between familiar humans and familiar conspecifics (Peirce et al. 2001). Interestingly, electrophysiological studies have shown that human and dog faces, despite large morphological differences, activate the same neurons in the sheep brain, presumably because both are seen as a potential threat. However, familiar

humans with positive associations become encoded in the same cell populations as familiar sheep from the herd (Kendrick 2006). Similarly, recent research has shown that when dog experts view social interactions between dogs or people, the right posterior STS is activated whereas this area is only activated by the sight of human interactions in control subjects (Kujala et al. 2011).

In contrast to the extensive research conducted looking at the lateralisation of auditory and visual discrimination/recognition of individuals, there has been no research looking at the spontaneous cross-modal recognition of individuals by animals. Two studies to date have investigated hemispheric specialisation during learnt audiovisual matching tasks. Rhesus macaques that learnt to associate 6 non-biological sounds with 6 visual patterns were significantly impaired when lesions were made in the left hemisphere, particularly in the auditory cortex but were unimpaired if the lesions were performed on the right hemisphere (Gaffan and Harrison 1991). The other study, of social perception, trained dolphins to associate audio stimuli including known signature whistles, human voices and tones with visual objects including videos of dolphins and people. They found that, although there was no eye preference in viewing the stimuli, dolphins were significantly better at matching the audio-visual stimuli if the objects were viewed by the right eye (Delfour and Marten 2006). This study also suggested that the type of audio-visual stimuli (conspecific, heterospecific, non-biological) did not affect lateralisation. The left hemisphere bias during these tasks may reflect the role this hemisphere plays in template matching and the categorisation of familiar objects (Rogers 2008; MacNeilage et al. 2009; Rogers 2010).

In horses lateralisation has been found in motor responses (McGreevy and Rogers 2005; Murphy et al. 2005; Austin and Rogers 2007; Williams and Norris 2007; Murphy and Arkins 2008) and effects of tactile stimulation (Des Roches et al. 2010) as well as olfactory behaviour (McGreevy and Rogers 2005). However, there has been only one study of auditory lateralisation to date, showing a right ear (left hemisphere) preference for the processing of calls from familiar non-group members but not for group members and a weak right

hemisphere bias for strangers' calls (Basile et al. 2009). In the visual domain, LaRose et al. (2006) found that, although there was no strong overall eye preference for the viewing of a novel inanimate object, the most emotionally reactive subjects preferred to view the objects with the left eye (and some of the less emotional subjects actually used their right eye preferentially), suggesting that when the novel object is viewed as potentially threatening the right hemisphere is activated. These findings were further supported by research demonstrating that horses view objects with negative associations with their left eye; neutral/novel objects were viewed with the right eye and positive objects were not viewed with either eye preferentially (Des Roches et al. 2008). These results support the valence hypothesis of lateralisation. This preference to view novel objects with the left eye appears to extend to unfamiliar people, although a weaker preference to view familiar people with the left eye has also been reported. In an interactive setting, horses tended to prefer to approach both familiar and unfamiliar people with them in their left visual field (Farmer et al. 2010). This has been interpreted as reflecting the right hemisphere's dominance in situations that require quick reactions, but may also represent a motoric bias.

Section summary

It is clear that the ability to discriminate and appropriately categorise conspecifics and some heterospecifics is crucial to the survival of individuals in many animal species and there is now extensive research showing how different species have the capacity to recognise various groups such as kin, neighbours and offspring. Individual recognition is the most fine-grained classification of social partners and is believed to be widespread among animals, from insects to birds and mammals. However it is hard to prove conclusively that an animal is recognising specific individuals rather than just discriminating between them on the basis of differing levels of familiarity.

Most unimodal studies of the categorisation of individuals typically involve presenting subjects with stimuli from different conspecifics or heterospecifics and looking for variations in the subjects' behavioural responses. The resulting

behaviour may be based on either a specific mental concept of the individual, differing familiarity levels or a form of associative learning. No matter how small and fine-grained the categories of individuals discriminated, one cannot conclude that an animal is capable of true individual recognition unless it can be shown that the current sensory cues appear to activate a unique internal representation of the signaller. At the beginning of this section I explained that individual recognition involves not only discriminating between identity cues at the level of the individual rather than a broader classification, but it also involves the matching of current cues with information about that specific individual that is stored in memory.

The major problem with the operant conditioning and matching to sample methods is that, although they can be used to demonstrate that animals have the potential to discriminate between identity cues at the level of the individual, they do not demonstrate that these current sensory cues act to retrieve stored information about that individual. As such the method lacks ecological validity. A wide variety of species, with sufficient visual acuity and basic learning mechanisms, can discriminate between individual identity cues without performing these social discriminations naturally. For example, bees are able to discriminate between the faces of different humans, demonstrating how a species unlikely to spontaneously discriminate heterospecific individuals visually, and possessing a small brain, is capable of making these apparently complex discriminations (Dyer et al. 2005). This serves to emphasize the importance of investigating the mechanisms by which such discriminations are made, the ecological importance of these skills to a species and the extent to which discriminations go beyond simply identifying stimuli with similar physical properties.

To demonstrate that identity information is salient and actually serves to categorise social partners in a meaningful way, it is necessary to show that this information is associated with socially relevant information about the individual such as dominance rank or kinship. Field studies, such as those mentioned above, have shown that both conspecific and heterospecific identity cues are highly salient to a wide number of species and are associated with important

social information such as rank, familiarity, reliability or threat level. However, in field studies it is hard to determine whether individual recognition is the mechanism by which the complex categorisation of others occurs.

An ideal way to demonstrate individual recognition is to show that an animal can spontaneously combine specific individual identity cues across senses because this indicates that cues are stored in some form of higher-order representation that is unique to that individual and independent of modality and the physical properties of the stimuli. It should be noted that by higher-order I refer to advanced and complex processes that integrate and synthesize information from a variety of sources and occur further along the neural pathways, after initial and basic sensory processing. Neurophysiological evidence suggests that cross-modal processing activates the higher-order V5 visual areas and auditory areas simultaneously in conjunction with other areas of association cortex, and in the case of individual recognition, with corresponding activation of memory and emotions. The preferential looking and expectancy violation paradigms, developed originally for studying concept formation and knowledge acquisition in pre-verbal infants, provide promising ways to assess this ability in animals. By providing subjects with the cross-modal identity information from more than one highly familiar individual, rather than a stranger and familiar individual, as has been studied before, we can determine whether animals are truly capable of matching multi-sensory cues to individual identity. With this method it is possible to establish that recognition is not based on degrees of familiarity or any other broader category than the individual. This is the aim of Articles I and II in this thesis. I also investigate the neural bases for spontaneous cross-modal individual recognition by looking for orienting asymmetries and differences in discriminatory ability when social partners are seen in the left or right visual field.

I now turn to the second field of social cognition that this thesis covers, that of obtaining information from human social partners.

Obtaining information from human social partners

Introduction

For horses, humans represent significant social partners and anecdotally horses are good at reading human signals, as the case of Clever Hans famously demonstrated. Hans was a horse who was able to pick up such subtle and unconscious cues from his trainer and other people that he convinced a number of researchers that he was able to perform calculations, spell words and answer questions. What he was in fact doing was reading tiny muscle movements that his handler and viewers unintentionally gave when Hans had given the correct answer (Pfungst 1907 as cited in Waring 2003). Clever Hans was the first animal to really demonstrate just how much some species can pick up on human signals even when they are minute and being given unconsciously. The case of Clever Hans is now cited in psychology classes as an example of the dangers of designing experiments in which the subjects interact with experimenters that are aware of the rationale of the study. In spite of this, or perhaps because of it, social cognition in horses has hardly been studied.

In the last decade however, there has been a growing interest in the study of human-animal interactions. In this section I outline the research looking at the ability of animals to read human-given cues and then outline the various hypotheses put forward to explain the pattern of results across species.

Attributing attention

An important social skill for group living animals is the ability to determine the direction of other individuals' attention. This allows animals to engage in more effective communication, to avoid performing behaviours that may cause aggression from others if observed, to follow the gaze of others to significant events, and to detect when predators are observing them.

It has been suggested that the ability to detect eye direction and attribute attention is an ontogenetic and phylogenetic precursor to theory of mind and language abilities in humans, following clear developmental stages in both human infants and primates (Baron-Cohen 1994; Povinelli and Eddy 1996; Ferrari et al. 2000; Itakura 2004). Human infants from an early age have an appreciation that " the eyes are the key to attention" and will preferentially use eye rather than head or body cues when following the gaze of another (Tomasello et al. 2007). By 18 months they will preferentially ask for food from an attentive person using body, head or eye cues and between 18 months and 3 years they begin to develop a mentalistic understanding of attention (Gomez 2005; Doherty 2006). Gaze sensitive areas of the human and primate brain have also been located (Emery 2000).

There is currently much interest in discovering the prevalence of attention attribution skills across taxa, specifically in determining the cues employed by different species, and the extent to which animals have a mentalistic understanding of attention. A large number of species (e.g. goats, *Capra hircus*, Kaminski et al. 2005; rhesus macaques, Ferrari et al. 2000; gibbons, *Hylobates agilis*, Myowa-Yamakoshi and Tomonaga 2001; great apes, Tomasello et al. 1998; Brauer et al. 2005; dolphins, Pack and Herman 2004; dogs, Brauer et al. 2004; McKinley and Sambrook 2000; ravens, *Corvus corax*, Bugnyar et al. 2004; tortoises, *Geochelone carbonaria*, Wilkinson et al. 2010b; horses, Rossiter 2010) are able to follow the gaze of others, however, detailed research into the knowledge animals have about the visual perspective of others and how flexible their behaviour can be in the light of this knowledge, has only been conducted in a few species.

The sensitivity of a number of Corvid species, including ravens and western scrub jays (*Aphelocoma californica*), to the attentional states of others has been studied in such detail. Both species cache food and also pilfer the caches of others; as such it would be highly adaptive to be sensitive to the gaze of others. Scrub jays are aware of whether they are being watched and cache their food in places out of sight or further away when a conspecific is watching (Dally et al. 2004; 2005). Birds that have been thieves themselves are more likely to take

this preventative action or to subsequently recache food, suggesting that they are aware of the onlooker's intentions and are using past experience to predict the future actions of conspecifics (Emery and Clayton 2001). Scrub jays distinguish who is watching them and hide food from dominants but not partners and also distinguish between knowledgeable and ignorant conspecifics, altering their recaching behaviour in the light of this knowledge (Dally et al. 2006). Ravens also distinguish between knowledgeable and ignorant potential pilferers, and distinguish between conspecifics that were present during caching and could observe the cacheing behaviour and those that had their vision occluded by a barrier. The findings also confirm that this differentiation between knowers and guessers is due to a sensitivity to others' viewpoints rather that to any behavioural cues given by knowledgeable conspecifics (Bugnyar and Heinrich 2005; Bugnyar 2011). The ability of ravens to attribute attention to others extends to human experimenters and subjects are able to adjust their position to follow a person's gaze around a barrier (Bugnyar et al. 2004; Schoegl et al. 2007). They are also sensitive to the competitive or cooperative intent of human experimenters when cacheing food, only modifying their cacheing behaviour in front of pilferers (Bugnyar et al. 2007).

To be aware when someone is attending to you, there are a number of cues that could be used from gross cues such as body orientation to finer cues such as head orientation and eye direction. When hand-reared jackdaws (*Corvus monedula*) were presented with valuable food they took longer to retrieve the reward if an unfamiliar, and hence threatening, person observed them. In this paradigm they were sensitive not only to body and head orientation but also to eye direction (von Bayern and Emery, 2009). A number of studies have shown that with human experimenters at least, dogs, in line with human infants, also have a good understanding of the relationship between the eyes and attention (McKinley & Sambrook, 2000). Dogs are more likely to obey commands when the owner's eyes are open compared to when they are closed or when humans are looking at them rather than looking away (Call et al. 2003). Similarly, dogs will beg for food from an experimenter whose eyes are visible rather than an experimenter who is blindfolded. In a fetching task dogs showed more hesitant behaviours and were less likely to fetch an object when the person's eyes were

covered (Gácsi et al. 2004). Additionally, dogs only use gaze if it is specifically at the target, suggesting that they may have some form of appreciation of the communicative intent underlying the cue (Soproni et al., 2001). Dogs have also been shown to be able to distinguish between effective and ineffective barriers to a handler's sight and to only steal food when it is out of sight of the handler (Brauer et al. 2004).

Puzzlingly, great apes seem good at following gaze in some contexts but perform surprisingly poorly on many other tasks aimed at assessing their ability to read human cues. They are able to follow the gaze of a human around barriers towards an object that is out of their immediate sight (Brauer et al. 2005) and chimps are also aware of when barriers occlude a person's view of themselves (Hare et al. 2006). Thus apes appear to have some knowledge of what others can and cannot see and possess a rudimentary understanding of the relationship between seeing and knowing (Hare et al. 2001; Bulloch et al. 2008). Despite this, chimpanzees appear to rely on head and body cues when determining when a person is attending to them in a begging task and are unable to spontaneously use eye cues (Kaminski et al. 2004; Tempelmann et al. 2011). One study showed that while chimpanzees were able to learn to gesture when a human face was visible they did not learn to gesture only when the eyes were visible (Reaux et al. 1999). In contrast, other studies have shown that chimpanzees are capable of distinguishing between an attentive and inattentive person on the basis of the visibility of their eyes in a begging task without extensive training (Bulloch et al. 2008).

Studies that have employed different methodologies have also shown that primates are sensitive to the importance of eyes in determining the direction of another's attention given certain situations. In a competitive food paradigm, rhesus macaques selectively chose to steal the food from the human experimenter using not just body or head cues but also eye cues (Flombaum and Santos 2005). A sensitivity to eye cues during a competitive food task has also been demonstrated in olive baboons (*Papio anubis*) (Vick and Anderson 2003). In a study of 116 captive chimps, Hostetter et al (2007) observed the begging behaviours of subjects when experimenters had their eyes open or

closed. They found that chimps produced more visual communicative gestures when the person could see them and more vocalisations when they had their eyes closed. A similar study of capuchin monkeys has pointed to a discrepancy between the accuracy of the overt response to cues and more unconscious measures of responding such as looking time (Hattori et al. 2007). Here there was no difference in the number of visual begging behaviours given by the subjects when the experimenter was looking at them or looking away but analysis of their looking time revealed that they looked for longer at the experimenter when her eyes were open compared to when they were closed. Thus it is currently unclear whether these apparently contradictory results are due to a lack of motivation, are a methodological artefact, or represent a genuine lack of sensitivity (Barth et al. 2005; Hare and Tomasello 2004; Hattori et al. 2007).

Using human-given communicative cues

The object choice task is a paradigm that has been widely used as a method of assessing animals' abilities to use the communicative cues of humans. A subject is presented with the choice of two or more containers and a demonstrator indicates which of the containers the subject should choose. The cues that have been used to indicate a correct choice in these experiments are varied, and include the use of gaze, body orientation, pointing, markers and touch.

In the object choice task dogs have shown a level of accuracy and flexibility that has not been seen in other species to date (Hare et al. 2002). Pointing is predominantly a human cue that is almost never seen other species in their natural environment (except a single report of a wild bonobo pointing and, arguably, pointer dog breeds) but it has been observed frequently in captive apes (Veà and Sabater-Pi 1998; Leavens et al. 2005). Despite this, dogs use human pointing and a wide variety of other human-given cues from the first trial of an object choice task (Miklosi and Soproni 2006). Not only are they able to use cues such as proximate sustained pointing (pointing near the target that continues until the choice is made) and touching, that provide stimulus

enhancement, but they are also able to use cues such as distal momentary pointing (temporary pointing at a distance from target), body orientation and, in some cases, gaze (Hare and Tomasello 1999). However, cues that protrude from the human's body and are closer to the container are more salient, with, for example, elbow pointing (keeping the hand on the chest and protruding the elbow) or cross-body pointing (pointing with the contralateral arm across the body) being less informative than pointing with the whole arm (Lakatos et al. 2009). Dogs are also highly adaptable in their use of cues and can generalize to new gestures and the use of markers. Dogs are even able choose the container which an experimenter is pointing to when the person is closer to, and walking towards, the other container (Soproni et al. 2002).

Studies into the ontogeny of this skill in dogs demonstrate that puppies are able to use a variety of human cues in the object choice task from a early age irrespective of whether they have been litter reared or reared in a human home (Hare et al. 2002). By 6 weeks puppies can use proximal pointing and by 2-4 months they can use distal momentary pointing (Gácsi et al. 2008; Riedel et al. 2008; Virányi et al. 2008). In contrast, in the majority of studies of hand-reared wolves, subjects have performed less well (Agnetta et al. 2000; Hare et al. 2002). Young wolves are unable to use distal momentary pointing although they can use cues that involve stimulus enhancement such as proximal pointing or touching. Through extensive training they can also learn to use the distal point cue (Virányi et al. 2008). Research comparing silver foxes (*Vulpes vulpes*) that have been selectively bred over a number of generations to be less fearful and aggressive to humans, to those that have had no selective constraints on breeding, has shown that the domesticated foxes are as good as dogs and better than their unselected relatives at reading human cues (Hare et al. 2005). Overall, these findings have led to the suggestion that selection pressures during the process of domestication produced enhanced "human reading" skills in dogs, however, no other domestic animal has been extensively studied (Hare et al. 2002).

Horses have been shown to use the presence of a person as a stimulus enhancement cue to locate hidden food (Krueger et al. 2011). In a small study

of four horses, two of the animals could use the touching of the container and one used dynamic sustained pointing as a cue (moving the hand up and down in the direction of the bucket until the choice was made) (McKinley and Sambrook 2000). This poor performance by the horses does not fit well with the domestication theory of social cognition. In a more extensive study, horses were able to use proximal pointing cues and also a distal pointing cue providing it was sustained while the choice was made. They were unable to use the distal momentary point (Maros et al. 2008). No other cues have been tested to date. In one study domestic cats (*Felis catus*) were found to perform at a comparable level to dogs from the first trial, using pointing gestures including the distal momentary point (Miklósi et al. 2005). Although they do not have such a close relationship with people than dogs or cats, recent research has shown that goats are also able to use distal sustained pointing cues in an object choice task but unlike dogs they could not use head direction and gaze (Kaminski et al. 2005).

Again primates tend to perform surprisingly poorly in object choice tasks. In a number of studies primates have been unable to reliably follow any human cues provided including tapping, pointing, gaze and marker placement (Tomasello et al. 1997; Hare et al. 2002; Byrnit 2009). Some primates are able to follow basic pointing cues that provide stimulus enhancement but do not use cues such as gaze and distal momentary pointing (Anderson et al. 1995; Povinelli et al. 1997; Miklosi and Soproni 2006). Often subjects require a number of trials to learn to use the cues and once the task is learnt their behaviour is inflexible (Itakura et al. 1999; Hare and Tomasello 2005; Byrnit 2009). However, results from highly enculturated subjects suggest that extensive socialisation can improve abilities (Miklosi and Soproni 2006). In addition, although apes do not appear to readily use such a wide variety of cues in the object choice task as dogs, chimpanzees and orangutans (*Pongo pygmaeus*) trained in the task then distinguish between accidental and intentional cuing (Call and Tomaello 1998). This suggests that they are capable of appreciating the communicative intent behind these cues. In contrast, dogs don't distinguish between accidental and intentional cuing (Riedel et al. 2006) although there is some evidence that dogs respond differently to knowledgeable versus ignorant people in the object choice task

and when gaining a person's attention to locate a hidden toy (Viranyi et al. 2006; Maginnity 2007).

It is also important to note that minor differences in methodology change the responding of primates in social cognition tasks, with subjects reliably using gaze alone when they are able to approach the experimenter compared to performing at chance levels when remaining inside a test box (Barth et al., 2005). Differences in the distance between the subject, experimenter and containers have also been shown to have a large effect on performance (Mulcahy and Call 2009). If the object choice task is set up as a competitive situation in which subjects are presented with two containers and are in competition with the experimenter to obtain food then chimpanzees that fail to use pointing cues in a cooperative context have been shown to spontaneously respond to cues such as reaching (analogous to pointing in a communicative situation) (Hare and Tomasello 2004).

Another group of wild animals, however, have proven to be particularly adept at this task - marine mammals, specifically dolphins (Pack & Herman, 2004; Tschudin et al., 2001) and seals (Scheumann & Call, 2004; Shapiro et al., 2003). All subjects tested have been highly enculturated and trained extensively and, like dogs and cats and unlike many of the apes studied, they were able to perform at high levels from the first trials, able to use distal pointing cues and to be flexible in their use of novel cues. The seals were also able to use asymmetrical pointing, where the person is standing closer to the empty container while pointing to the target container. These results suggest experience may at least be one route to success in this task.

Finally, a number of bird species have also been studied. Jackdaws were found to be sensitive to eye direction in a competitive version of the task but only followed a distal pointing cue, not eye gaze or head direction in a cooperative context (von Bayern and Emery 2009). Ravens have been shown to use touching but not pointing or gaze cues (Schloegl et al. 2008). Captive African grey parrots (*Psittacus erithacus*) can use proximal pointing but not distal pointing or gaze (Giret et al. 2008). Perhaps surprisingly, non-social Clark's

nutcrackers (*Nucifraga columbiana*) were able to spontaneously use tapping cues and learn a point cue after very few trials, but could not use a gaze cue. Thus they perform to a similar level as the more social corvids and parrots (Tornick et al. 2010).

Theoretical explanations of results

There is much debate concerning the factors that may serve to facilitate these human-reading abilities across different species; in particular the extent to which the skills are learnt through exposure to humans during an animals' lifetime and which evolutionary pressures determine levels of performance in different species. In this section I outline the main hypotheses put forward to try to explain inter and intra-species differences in the pattern of responding.

The domestication hypothesis

The domestication hypothesis states that domestic dogs (and perhaps other domesticated animals), through a process of convergent evolution during the domestication process, have become particularly skilled at comprehending human communication (Hare et al. 2002). Furthermore it has been suggested that these improved social skills have not developed through specific selection for this skill but rather as a by-product of selection for tameness, as demonstrated by the selective breeding of silver foxes (Hare et al. 2005). This produced a strain of foxes that were not only as good as dogs at reading human cues but, within very few generations, they also underwent morphological changes that made them look more like domestic dogs. These results lend strong support to the domestication hypothesis and are also a striking example of how adaptation for one discrete trait can lead to a large variety of physical and behavioural changes in a species, and within a remarkably short amount of time. This general increase in tameness would facilitate the acceptance of humans as social partners, and therefore give dogs a general predisposition to pay attention to and learn human given cues, although such a predisposition may itself be facilitated by an underlying genetic propensity as scroungers to attend to the actions of others (Reid 2009).

It seems likely however, that dogs underwent a two-stage process of domestication, an initial generalised selection for tameness followed by breed diversification in which specific traits were selected, depending on the role of the breed (Cooper et al. 2003; Hare and Tomasello 2005). These breed-specific traits could have included an ability to respond to the communicative cues of human partners. This is supported by findings that primitive dogs that have undergone only the first stage of domestication, such as dingoes (*Canis dingo*) and the New Guinea Singing Dog (*Canis hallstromi*) appear to be intermediate between wolves and dogs in their ability to use human cues in an object choice task (Wobber 2005; Smith and Lichfield 2010). In addition, one study found that breeds strongly selected to work with humans were better at reading human cues than breeds in which this skill had not been strongly selected for (Wobber et al. 2009). However, such a conclusion should be made with caution as it is also possible that the size of the dogs affected their ability to use certain cues since both of the working dogs were larger than the non-working dogs in this study and size has been shown to affect a dog's ability to use facial cues in an object choice task (Helton and Helton 2010).

The majority of studies conducted so far have shown that domestic dogs are better at reading human cues than wolves given the same rearing environment. A closer analysis of the relationships of dogs and wolves with humans has revealed several behavioural differences in the interactions of these two species with people that may account for their different abilities to respond to human cues. One such difference is that dogs actively look towards humans to gain information. When dogs and hand-reared wolves are presented with an insoluble task, dogs look towards the experimenters for cues and assistance whereas the wolves tend to try to solve the problem unaided. Miklosi et al (2003) conclude that this "simple reason produces the big difference" between dog and wolf comprehension of human cues. Dog puppies also tend to produce communication signals directed at humans such as attention seeking barking from an early age whereas hand reared wolf puppies do not. Although wolf pups did prefer to be in close proximity to their caregiver they also displayed more aggression towards them than dog puppies (Gacsi et al. 2005).

Obviously domestication is not a homogenous process across species but all domestic species would have undergone some selection for increased tameness, akin to the first stage hypothesized for domestic dogs. The fact that goats with little experience of human contact and which undoubtedly have not been selected specifically to read human communicative cues in the same way as dogs, also show some skill in these tasks, lends support to the domestication hypothesis (Miklósi et al. 1998). However, the goats would certainly have had experience of food provisioning by humans and may have developed an association between human hands and food. It remains to be seen however, whether all domesticated species perform better than their wild cousins if they are socialised to comparable levels. So far this direct comparison between a domesticated species and its wild counterpart has only been conducted with dogs and wolves.

However, the domestication hypothesis is built on several fundamental assumptions that have recently been called into question. One assumption is that domestic dogs are more skilled at reading human given cues than wolves given the same rearing history. Research has now shown that adult wolves with daily human interaction are able to use the distal momentary point cue, the benchmark for demonstrating cue use beyond the use of basic stimulus enhancement cues (Udell et al. 2008). While this ability does appear to take longer to develop in wolves, there is growing evidence that older subjects are able to use the cue without extensive training (Gácsi et al. 2009). Success was attributed not only to rearing environment but also to the subjects being tested outside. The picture is further confused by recent findings that juvenile hand-reared wolves are better than juvenile dogs at following both dog and human gaze cues in an object choice task but were not better at following human pointing. In addition, these wolves were also more successful than the dogs at opening a box when presented with either dog or human demonstrators, suggesting the wolves may actually be more attentive to the actions of others (Range and Viranyi 2011).

A second premise of the domestication hypothesis is that domestic dogs have a genetic predisposition to be good at reading human cues and require very little or no experience with humans for this to develop. This notion has been supported by studies such as that of Riedel (2008) which showed that dogs as young at 6 weeks could follow basic human pointing gestures, however, even very young puppies are likely to have had significant exposure to humans and there is some debate as to whether the results show a small improvement with age (Wynne et al. 2008; Hare et al. 2010; Udell and Wynne 2010). It has also been reported that stray dogs, that have not had significant experience with humans, are unable to use the distal momentary point although they can use more basic cues (Hare et al. 2010; Udell et al. 2010a).

The Canid generalisation hypothesis

An alternative to the domestication hypothesis is the suggestion that domestic dogs have inherited certain abilities and traits from their wild ancestors that have made them predisposed to be good at reading human cues (Hare et al. 2002). While the majority of research to date points to improved abilities of domestic dogs, wolves are also beginning to demonstrate some ability to successfully respond to advanced cues. Furthermore, the domestication and canid generalisation hypotheses need not be mutually exclusive. There may have been features of wolves that made them particularly good candidates for adapting to a close relationship with man, for example their role as cooperative hunters. This theory may also extend more generally to domestic animals. Comparatively few animals have been domesticated, which suggests that the features an animal must possess to be conducive to domestication may be relatively rare. Most domestic animals are naturally social and live in groups with clear dominance hierarchies; this feature for example, may enable humans to superimpose their presence onto this dominance structure (Mignon-Grasteau et al. 2005). In the case of horses, it may also be that they are sensitive to human behaviour because in the wild, equids live in heterospecific groups of prey species and use cues from other species in the detection of predators (Goodwin 2002).

The cooperation-competition hypothesis

Hare and Tomasello (2004) have argued that the poor performance of chimpanzees in standard object choice tasks reflects the unsuitable nature of the task rather than a lack of cognitive ability. They believe that chimps are inherently competitive in nature and so do not perform well in tasks involving cooperation. Thus discrepancies between different tests can reflect species-specific constraints highlighted by the nature of the experimental design. As mentioned previously, primates have been shown to perform better in competitive than in cooperative situations and in some studies appear to possess a mentalistic understanding of others' behaviour (Hare et al. 2000; Hare and Tomasello 2004). For example, apes that were trained to use a marker placed by an experimenter only used this cue if it appeared that the experimenter placed the marker intentionally rather than by accident, suggesting that some primates are sensitive to the intent underlying human action (Call and Tomasello 1998).

The emotional reactivity hypothesis

The fact that tameness appears to affect ability to read human social cues shows how temperament may constrain social cognition. Hare and Tomasello (2005) have synthesized their theories of domestication and competition-cooperation into the emotional reactivity hypothesis. They suggest that the ability to read the communicative cues of others depends on the degree to which the species shows inter-individual tolerance. Hence to be adept at reading human cues, an animal must be able to accept people as social partners. Hare and Tomasello suggest that complex human cooperation is only possible because of our unique temperament. They suggest that human evolution involved a form of "self-domestication" in which selection was made by groups for tamer members with less emotional reactivity. Those people that were too aggressive and competitive were excluded from societies. This remains a highly speculative theory that currently has no direct evidence and has merely been extrapolated from the results of the silver fox experiments. A

comparison of bonobo and chimp social cognition could serve to test this hypothesis more directly because these species are very similar except that bonobos are a lot more socially tolerant. If bonobos were found to have better social skills than chimps then this would be the first empirical data lending support to this theory.

As prey animals, horses are likely to have a higher level of emotional reactivity towards man than dogs and according to the emotional reactivity hypothesis this would lead to a reduced ability to read human cues. The nervous temperament of horses may be why they perform badly on many cognition tasks. One suggestion for future research in dogs and humans that could also be conducted with horses is an assessment of the correlation between temperament (emotional reactivity) and social problem solving skills (Hare & Tomasello, 2005).

The enculturation hypothesis

The ability of dolphins and seals to use complex communicative cues such as gaze and distal pointing demonstrates the potential importance of enculturation in understanding the signals of another species. Unlike primates, marine mammals are phylogenetically distant to humans and, unlike dogs, they are not domesticated, yet they are highly proficient at reading human gestures. As with the effects of domestication, the extent to which enculturation fosters these skills will also depend on species-specific constraints.

Although the results from apes are more mixed those those from marine mammals (Miklosi & Soproni, 2006), highly enculturated language-trained apes that are typically raised alongside humans do appear to perform better than many institutional populations tested. Bulloch et al (2008) believe their chimps performed better on the object choice task than those tested by Reaux et al (1999) because, although both were populations from primate centres, the subjects tested by Bulloch were much more enculturated. It is also important to note that many of the primates studied in an institutional setting were wild caught, having quite possibly witnessed the slaughter of their mother and group

mates, had not been socialised with humans when young and then were kept in extremely impoverished environments in laboratories. It is now very evident from human psychological studies that early trauma and impoverished environments can have an extremely detrimental effect on the cognitive and social development of children. This institutionalised population of primates is hardly representative of the species as a whole and yet is widely studied across all fields of comparative psychology (Leavens and Racine 2009; Leavens et al. 2010). A direct comparison between domestic dogs and language-trained apes is far more appropriate than between dogs and most institutionalised apes.

Experience with humans also appears to be important in the cognitive performance of horses (Henry et al. 2005). In a pilot study, horses trained with a more positive technique emphasising natural cues, were better at the object choice task that those trained with more traditional techniques based on negative reinforcement (McKinley and Sambrook 2000). However, in a more extensive study, horses trained in a more "natural" way were better at completing the training phase but were not more accurate than the horses trained more traditionally when presented with a pointing cue (Bartosova et al. 2008). Clearly horses don't undergo the same intense enculturation process as dogs and are also trained in a rather different way, being ridden and with more emphasis placed on tactile cues. As such horses also provide us with an opportunity to learn more about the interaction between enculturation and the evolutionary process of domestication.

Section summary

There are likely to be a number of factors that influence the degree to which an animal is able to read human cues and these factors will affect different species to varying degrees. It is important to note that many of these hypotheses are not mutually exclusive. To more readily understand the evolution of these abilities it is vital to test a wide number of domestic and wild species and attempt to elucidate the factors at work in each situation.

Other than the domestic dog, no other domesticated animals have been extensively studied to date, so the study of horses will help to clarify the role of domestication in the development of social cognition and the ability to read human gestural cues. Horses are also prey animals rather than predators thus it would be interesting to compare the behaviour of horses and dogs in light of this difference. If horses are found to have a degree of skill in reading human cues then clearly the potential factors outlined above for dogs may equally apply to domestic horses. It may be that this skill was directly or indirectly selected for during domestication, or that horses inherited this skill from their wild ancestors, or that they learn to use human communicative cues during their lifetime.

In the following section I provide an overview of the study species, the domestic horse. I include an outline of the evolutionary history and domestication of the horse, its social organisation and behavioural repertoire. In the section summary I go on to provide a brief discussion of why the horse is an ideal model for the study of recognition abilities and the ability to read human communicative cues.

THE STUDY SPECIES: THE DOMESTIC HORSE

Brief history

Horses belong to the order Perissodactyla, or odd-toed ungulates, in which there are three extant families, Equidae, Tapiridae and Rhinocerotidae. Equidae is the only family in the sub order of Hippomorpha (Perissoldactyls with one toe and long legs designed for speed). Equidae itself consists of only one extant genus, Equus, which contains 9 species; two species of horse, the domestic horse (*Equus caballus*) and the Przewalski's horse (*Equus ferus przewalskii*), three species of zebra (*Equus quagga, Equus zebra, Equus gevyi*), three species of ass (*Equus africanus, Equus hemionus, Equus kiang*) and the domestic donkey (*Equus asinus*). There is some debate about whether domestic horses and Przewalski horses should be considered as subspecies of *Equus ferus* because although they can breed and produce fertile offspring, the domestic horse has a diploid chromosome number of 64 and the Przewalski horse has 66 (Waring 2003).

The earliest fossil assigned to the Equidae family dates back 54 million years and is of a multi-toed small mammal, *Hyracotherium* or *Eohippus*. The first truly horse-like species, assigned to the genus *Equus*, evolved during the Pleistocene era 2.5 million – 12,000 years ago. By the end of this era large herds of wild horses (*Equus ferus*) roamed across Europe, Asia and North America, adapted to grazing in temperate open grasslands. However, as the climate changed at the end of the Ice Age and the open plains were replaced with forests and tundra, the numbers of horses decreased. This was probably also as a result of extensive hunting by man. Wild horses became extinct in America around 8,000 years ago and were pushed to the fringes of deserts across Eastern Europe and Asia (Clutton-Brock 1999). Of the 7 extant species of wild equids, 5 are now on the list of vulnerable or endangered species (Moehlman 2002). By the middle of the twentieth century horses had become extinct in the wild and although they were thriving as a domestic species, the species of wild Przewalski horse was comprised of 31 captive animals, of which only 9 reproduced (Boyd and Houpt 1994). Through a dedicated breeding

program this number had risen to over 1500 individuals by 1995 and they began to be reintroduced to their native environment of Mongolia. It is clear that if horses hadn't been domesticated, they would not have survived to the present day.

Archaeological data indicates that horses were domesticated around 5,500 years ago in the Botai culture of Kazakhstan (Outram et al. 2009). Here, settled people were likely to have herded horses although there is some evidence that horses were also bridled. The domestication process is believed to have spread rapidly, based on multiple founders from diverse populations rather than selective breeding of limited stock (Vila et al. 2001). By 2,000 BCE the domestication of horses was widespread across Europe. Differences in the genetic variation of DNA passed along maternal and paternal lines suggest that a larger number of mares but very few stallions contributed to the domestication process (Lau et al. 2009).

The main changes that occur during domestication are adaptation to man and man-made environments, coupled with the morphological and behavioural side-effects of artificial selection for increased production or performance (Andersen et al., 2006). Selective pressure from other factors such as predation and the need to seek food and shelter is relaxed. Domestication also tends to require greater social flexibility, with groups often being of a different size, less stable or of a different composition to those found in the wild. With these changes, humans became important social partners along with conspecifics and the raising of the flight/fight threshold in response to human contact occurred (Jensen 2006). Many differences in behaviour are quantitative rather that qualitative. Researchers that study the effects of domestication on behaviour advocate the study of domesticated animals as niche species adapted to their particular environment (Andersen et al. 2006).

Horses were domesticated later than all of the other most widely domesticated species including dogs (probably around 12,000 years ago; Coppinger and Coppinger 2001), cats, goats, sheep, cattle and pigs (*Sus scrofa*) (all between 8-10,000 years ago; Vigne 2011). Of these main domestic species horses (and

cats) have undergone the least morphological changes (Clutton-Brock 1999). This is probably due to the fact that horses have been primarily domesticated for one function – to transport man and his belongings. They have not been subject to the changes associated with increased food production that other livestock have experienced, nor have they been subject to the extreme morphological changes that dogs have undergone during breed diversification for the fulfilment of different roles. It has been suggested that domestication reduces cognitive ability and the brain size of domestic horses is 14% smaller than that of the smaller Przewalski horse (Rohrs and Ebinger 1993). There have also been slight changes in conformation and large variations in size across breeds, but these differences reflect small variations in their roles such as whether they are draft horses or ridden, designed for speed or endurance. Coat colour has also become much more varied, with an increase in white pigmentation, a side effect apparent in many domestic species including silver foxes selectively bred for tameness. This colour variation arose around the time domestication began (Ludwig et al. 2009).

One reason why horses and donkeys may have been domesticated while other equids have not is that they appear to habituate to stimuli faster than zebras (McGreevy et al. 2009). Although zebras can be tamed and ridden, anecdotal reports suggest they remain unpredictable (Kiley-Worthington 1987). In terms of behaviour, sexual, social and communicative gestures seem to have changed very little and domestic horses can become feral very successfully. Many domestic species tend to maintain juvenile traits into adulthood such as curiosity, flexibility, submissiveness, playfulness and care-soliciting behaviour, as well as some morphological characteristics of the young of their wild ancestors. This "neoteny" is clearly seen in dogs that display high levels of playfulness throughout their lives (Udell et al. 2010b). The incidence of play in domestic horses compared to their wild cousins has not been studied but again, horses do not appear to display strong neoteny.

It has been estimated that there are now 60 million horses worldwide and between 600,000 - 1 million horses in the UK alone (DEFRA 2004). From being

on the brink of extinction at the end of the Ice Age, horses, through domestication, have now become a highly successful species.

Social organisation

Numerous populations of feral horses exist across the world, as well as a few reintroduced wild horse populations, and these provide insights into the natural social organisation of the species. Horses are long-lived mammals with a complex social system. Wild and feral horses have an unusual social structure - among mammals there are few species other than the horse that form year round mixed groups (Clutton-Brock 1989). Individuals live in either bachelor bands or small, largely stable, family bands consisting of a stallion (occasionally multiple stallions) and a number of breeding mares and their offspring (Linklater 2000). These bands have large home ranges that overlap with several other groups so horses associate to varying degrees with a large number of conspecifics. Occasionally bands will join up with other groups to form much larger aggregations of up to one hundred individuals either on a temporary or more permanent basis then disband again to forage separately. Ecological factors such as harsh winters and increased risk of predation may cause these formations of larger groups (TAKH 2006). As such, horse societies can be viewed as a society with a high degree of fission-fusion dynamics (Aureli et al. 2008).

There is a strict, usually linear, dominance hierarchy within the bands and between the bands in a herd (Linklater 2000). The more dominant individuals/groups have better access to food, water and shelter. However, agonistic behaviour rarely escalates to violence, with 80% of aggressive encounters in a free-ranging herd of feral horses being threats to bite given with the head alone; kicks or even kick threats were rare (Clutton-Brock et al. 1976). Even threats are rare and are generally about 1.5 incidences per horse per hour for feral, domestic and Przewalski horses (Budiansky 1997). Affiliative behaviour is far more common and highlights the importance of social bonds in horse society (Kiley-Worthington 1987). Dominant individuals are rarely the

most aggressive (McDonnell and Haviland 1995; Heitor and Vicente 2010). Stallions defend the group while traditional views of horse society suggest a lead mare controls the day-to-day activities of the band members and is usually the instigator of group movements (Tyler 1972; Feist and McCullough 1976). As such, horse societies have been described as matriarchal (Goodwin et al. 2009). However, recent research into group decision making in free-ranging Przewalksi horses found several group members contribute to group movements and that such movements appear to be based largely on shared consensus decisions. Initiators of group movements were often older and higher ranking females, (with stallions frequently moving the group at the onset of the breeding season) (Bourjade 2007). In feral horses, stallions and the older and more experienced individuals were followed more readily (Feist and McCullough 1976). Leaders in horse society therefore tend to be older but not necessarily the most dominant individuals (Tyler 1972; Waring 2003).

Domestic equids are rarely given the opportunity to display the behaviour of their feral or wild cousins. Many males are gelded and stallions are rarely kept with mares. As a result we cannot expect to see exactly the same social structures in domesticated groups. A linear dominance hierarchy is generally maintained in domestic horse groups, however the factors that determine this hierarchy are not clear (Lehmann et al. 2003). A study of a free ranging, domestic horse group containing mares and geldings revealed that they were split into two subgroups with the mares dominant over the geldings (Sigurjonsdottir et al. 2003). Age has also been found to correlate with rank in some studies (Tyler 1972; Wells and Goldschmidt-Rothschild 1979; Kimura 1998; Sigurjonsdottir et al. 2003) but in others, age did not determine rank for the adults although they were dominant over the juveniles (Houpt et al. 1978; Heitor and Vicente 2010). Similarly, the influence of size or height on dominance in equids is debatable, with some studies showing a correlation (Tyler 1972; Houpt et al. 1978) and others not (Clutton-Brock et al. 1976; Heitor and Vicente 2010). Reported differences in the temperament of individual New Forest ponies enabled smaller more aggressive mares to dominate larger ones, despite an overall tendency for larger ponies to be more dominant (Tyler 1972).

Horse societies are typified by strong bonds between individuals (Waring 2003). Throughout their lives individuals have one or two, occasionally three, preferred social partners, regardless of the size of the group in which they live. Both juvenile males and females disperse from their natal band and so these affiliations are rarely kin based. Stallions may also share the defence of a harem and access to mares with other males, although whether this constitutes genuine cooperation/alliance formation is debatable (Feh 1999; Linklater and Cameron 2000; Feh 2001). What is clear from studies of domestic, free ranging horses and feral horses, is that they tend to choose preferred associates that are of a similar rank (Clutton-Brock et al. 1976; Kimura 1998; Sigurjonsdottir et al. 2003). Preferred associates stay close when resting (Heitor et al. 2006) and were also preferred grooming partners in an Icelandic herd (Sigurjonsdottir et al. 2003) and among Scottish Highland ponies (Clutton-Brock et al. 1976). However, no such relationship was found in Japanese feral ponies (Kimura 1998) or in family bands of Camargue horses where grooming rates were very low despite associates remaining in close proximity (Wells and Goldschmidt-Rothschild 1979). Friendship with a higher ranking individual can allow lower ranking individuals to gain better access to food than would be expected from their rank alone (Budiansky 1997).

The social intelligence hypothesis predicts that individual fitness should be strongly influenced by social dexterity. In horses the importance of bonds between unrelated females has recently been highlighted by research showing that female feral horses that have strong bonds with other mares in their band have greater reproductive success than individuals that are not so socially integrated. Social integration was not based on age or dominance in this case (Cameron et al. 2009). Domestic horses deprived of social contact with conspecifics will readily form bonds with heterospecific social partners including man (Budiansky 1997).

Modes of communication

Horses are primarily visual animals and have good visual acuity, akin to 20/33 vision, better than both dogs and cats (Timney and Keil 1992; Budiansky 1997). It is therefore not surprising that horses display a wide range of both gross and subtle body cues when communicating with conspecifics and are likely to be highly sensitive to postural cues during heterospecific interactions as well. Frequent olfactory behaviours such as sniffing conspecifics, particularly when greeting them, suggests olfaction is also important in communication (Krueger and Flauger 2011). Touch, in the form of grooming, as well as the touching of the nose and other parts of the body, are important methods of social contact and this is, of course, the principle method of communication between man and horse, particularly when the horse is ridden. Horses have good hearing with an amplitude threshold of 7dB and are sensitive to frequencies in the 55Hz to 33KHz range, with maximal sensitivity between 1-16KHZ (peaking at 2KHz) (Heffner and Heffner 1983). Despite this, horses have a relatively impoverished vocal repertoire for a species with such complex social organisation. However, as has been observed with domestic dogs, domestic horses are more vocal than their wild counterparts, presumably because predation risks are relaxed and in a domestic environment group members are often removed from sight (Waring 2003).

In this section I briefly outline the visual, olfactory and vocal behaviours used in conspecific communication and the extent to which these can be used to discriminate between conspecifics. I will also discuss heterospecific communication and the extent to which horses are able to categorise human social partners using visual and vocal cues.

Visual communication

Horses are able to detect very subtle changes in body posture, not just in their own species but also in humans, as the case of Clever Hans demonstrates. They communicate with gross body movements as well as changes in body

tone and facial gestures or movements of single parts of the body. Detailed descriptions of individual behaviours are recorded in the equid ethogram (specifically of play and agonistic encounters) published by Sue McDonnell and colleagues (1995; 2002). Visual communication has changed very little during domestication. As with the communicative signals of many animals, the evolution of many of these cues is related to the original function of the behaviour. Behaviours that are attended to by other conspecifics will be selected for and may become social signals that are exaggerated and highly ritualised. Many agonistic behaviours, for example, are exaggerated threats, including flattening the ears and showing the teeth as a bite threat or lifting the leg as a threat to kick. Symbolic communication of dominance is important in horses to maintain a hierarchy without dangerous overt aggression. Agonistic encounters between stallions therefore are highly ritualised and involve acoustic, olfactory and visual behaviours, including parallel prancing akin to the parallel walk seen in red deer (McDonnell and Haviland 1995).

In general horses exhibit either high or low postural tone depending on their level of arousal. When excited the head and tail are raised and the gait may become more elevated. Submissive behaviours include the flattening of the tail to the body, again probably developed as a form of protection from rear attack, ears are also flattened and head is held low. Additional facial movements involving changes to ears, eyes, nostrils, lips and jaw as well as changes in skin contour around the mouth, eyes and nose and tail gestures convey more precisely the context of the signal (Waring 2003). It should be noted that although subtle facial expressions and small muscular movements are reliably produced by horses in certain contexts, there have been no studies to date assessing the extent to which these facial expressions are actually detected and interpreted by other conspecifics. They may also be biological adaptations to prepare the horses for the particular situation, for example, widening the eyes during fright to increase vision, and not have any meaning to the receiver.

Observations of horse social behaviour suggests that horses are capable of discriminating between each other visually and categorising each other on the basis of familiarity, hierarchy and possibly individual identity, although very little

formal research has been conducted and the characteristics used for visual discrimination are unknown. Indirect evidence that horses categorise individuals as dominant or subordinate based on visual cues is given by the finding that horses will only copy the observed behaviour of dominant individuals in a social learning task (Krueger and Heinze 2008). Categorisation of individuals based on colour has even been observed in one group of free-ranging feral horses in America. The individuals in this population possess a wide range of coat colours and stallions were found to recruit mares of a similar colour (Feist 1971 as cited in Waring 2003).

Anecdotal reports also suggest that horses visually discriminate between familiar and unknown individuals. When free ranging stallions were reunited with their mares after 1 year, they immediately approached their former mates within a large herd (Feh 2005). Stallions also reliably detect intruders and retrieve group members that have strayed into other bands (Budiansky 1997). In a controlled study of mare-foal recognition, attempts by both mares and foals to be reunited with each other were disrupted by the removal of visual cues in the presence of olfactory and acoustic cues (by placing one of them in a stable out of sight) but recognition was not affected by covering the mare or foal with horse blankets and a hood (Wolski et al. 1980).

Olfactory communication

Behavioural observations of horses suggest that olfaction is an important mode of communication. Stallions will produce faecal piles around their home range and will cover the eliminations of other group members with their own scent; the sniffing of faecal piles is an important ritualised part of stallion competitions (McDonnell and Haviland 1995). Sexual status is also conveyed by the scent of the mare, and trained stallions at stud will mount objects that smell of a female in oestrus (Kiley-Worthington 1987). However, when olfactory cues are masked, the sexual behaviour of experienced stallions is not strongly affected compared to when vision is blocked (Anderson et al. 1996). Group members will also roll in the same place, perhaps to adopt a group scent.

Horses also greet one another by sniffing each other's nostrils and then usually progressing along the body to the genital area, suggesting they gain important information about an individual from this action. Although one study suggests that olfactory cues may convey information about broad categories such as age or sex of donor but not individual identity (Hothersall et al. 2010), other studies suggest horses are capable of more fine-grained discrimination of conspecifics based on olfactory cues. Stallions discriminate between the faeces of familiar versus unfamiliar stallions and may also discriminate between the scent cues of individual mares (Marinier et al. 1988; Rubenstein and Hack 1992). The ability of mares and foals to discriminate between their kin and another mare/foal is also reduced when olfactory cues are modified (Wolski et al. 1980) and horses discriminate between specific individual competitors by spending more time investigating the samples from horses that are most aggressive towards them (Krueger and Flauger 2011).

Vocal communication

Vocalisations are commonly used by horses when individuals have become isolated from the group, to maintain group cohesion, during inter and intra-sexual displays or if they wish to signal to conspecifics that are not currently attending to them (Waring 2003). Horses produce a number of calls that appear to have distinct functions. The main calls given by horses are the whinny, the nicker and the squeal. Non-vocalised sounds include snorts, blows and snores. Researchers have also described additional and intermediate calls such as the sigh-nicker, the roar produced by some stallions when rejected by a mare in oestrus, and the scream, thus the horse vocal repertoire can to a degree, be seen as a continuum (Tembrock 1963; Kiley 1969, 1972; Tyler 1972). I will discuss the acoustic properties and function of the four main communicative sounds produced by horses, the whinny, the nicker, the squeal and the snort, focussing on the whinny, the long distance contact call used in Article I to assess whether horses are capable of cross-modal individual recognition.

A useful framework for analysing the acoustic structure of vocalisations is the source filter theory of bioacoustics (Fant 1960). The acoustic parameters of a

vocalisation can be categorised into those that are produced at the larynx, the source of the vocalisation, and those that are produced by the vocal tract during the filtering process. The fundamental frequency of a call is produced by the vibration of the vocal folds at the source and produces the pitch of the call whereas the resonances within the vocal tract amplify certain frequencies while dampening others, producing peaks of energy, called formants, that produce the timbre of the call. The fact that these characteristics are determined by the anatomical and physiological properties of the caller means that receivers are potentially able to derive information about the physical characteristics of the caller from these features i.e. indexical cues (Reby and McComb 2003). Differences in formant structure and pitch of specific individuals are likely to produce reliable inter-individual differences in the calls, akin to voice quality in humans.

The Whinny or Neigh

The whinny is a high amplitude tonal call that varies in length from approximately 0.5 to 2.8 seconds (Kiley 1972). There is a characteristic change in the fundamental frequency during the call within a range of 400-2000Hz. Whinnies have an initial highly tonal introductory phase where the frequency increases to a peak of approximately 2 KHz in roughly a second (Browning and Schiefele 2005). The second phase consists of a series of rapid tonal frequency modulations with a frequency that drops slightly and the final phase consists of an oscillating, deep, less tonal sound in which the fundamental frequency gradually drops to around half the original level. The final part of the whinny is essentially a nicker. The call is made with the mouth open, although it may close near the end of the call resulting in a drop in amplitude and tonality (Kiley 1972). See Figures 1a & 1b.

D.

E.
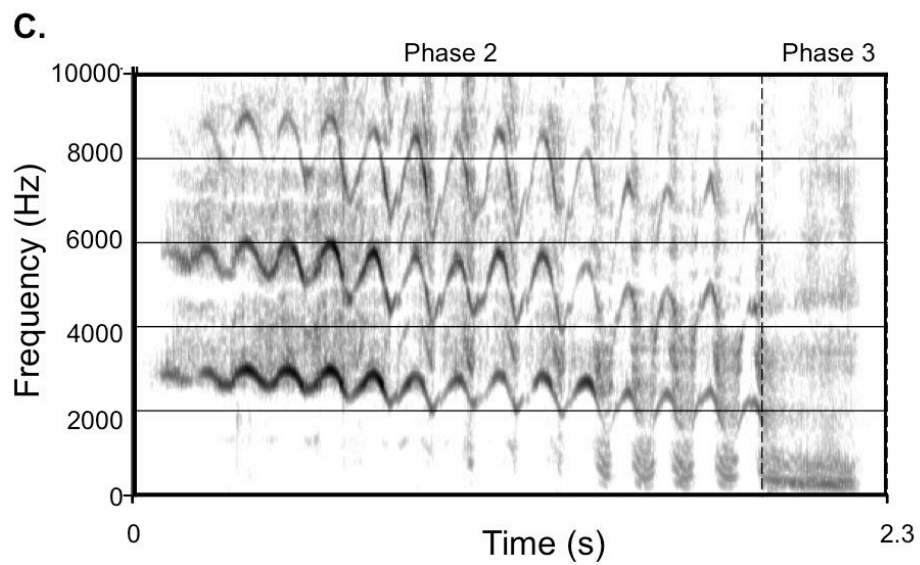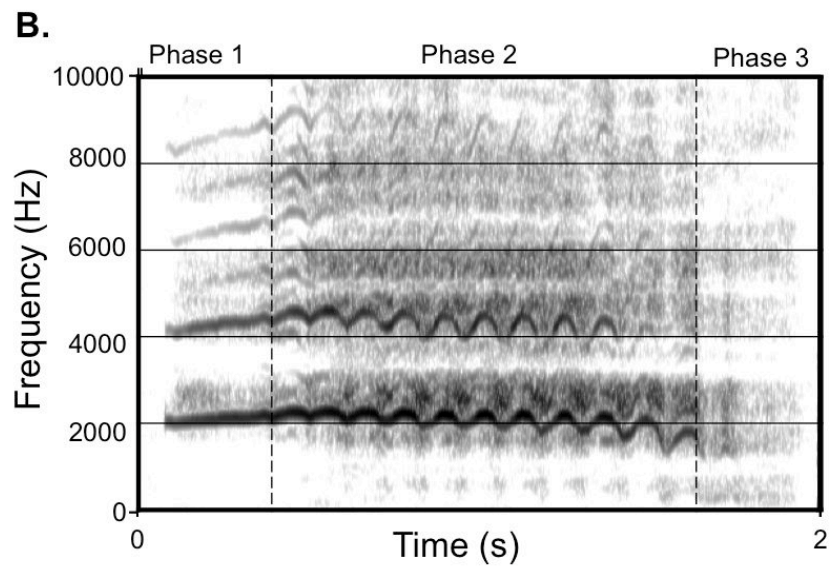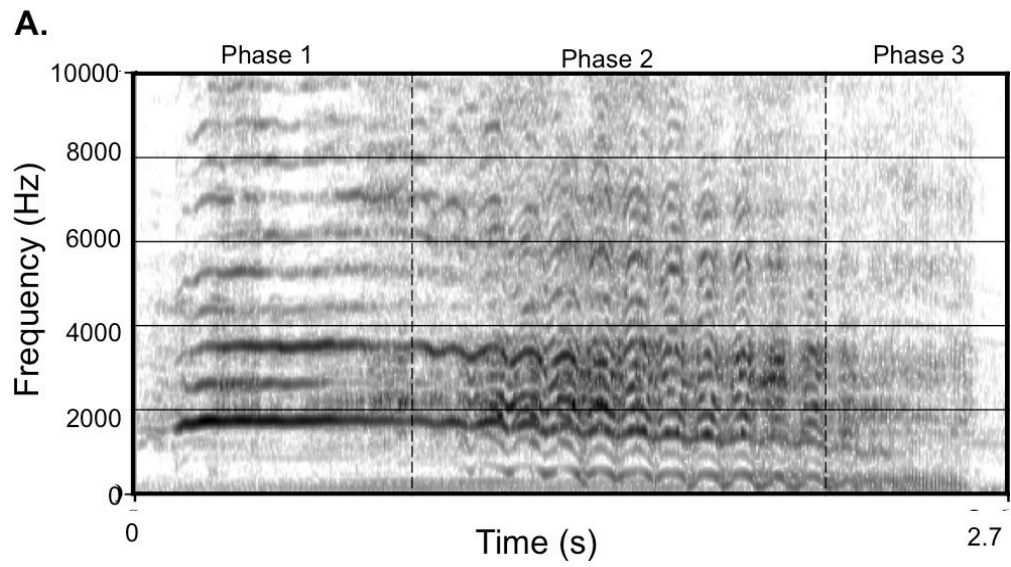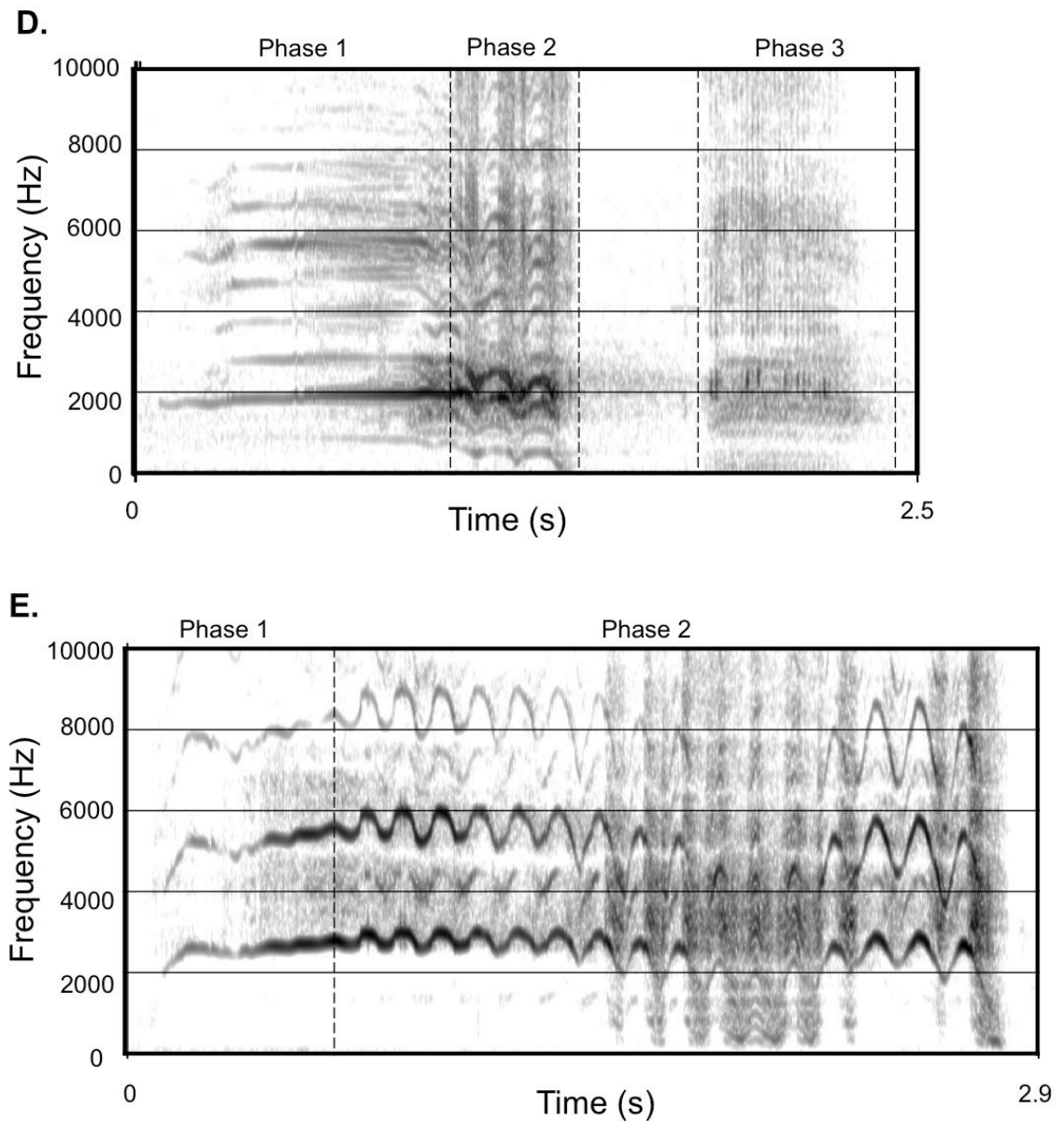
Figure 1: Spectograms of whinnies, providing examples of a typical whinny (A & B) and more idiosyncratic exemplars, including whinnies in which phase 1 is omitted (C), phase 3 is isolated from phases 1 and 2 (D) and phase 3 is omitted (E).

The whinny can be given in a variety of contexts although most commonly when a horse has been isolated from group members or a specific individual. Whinnies are also sometimes given when a threat is detected and stallions sometimes whinny to each other from a distance prior to a fight (Feist and McCullough 1976). Thus although in general the whinny typically appears to be given between group members as a cohesion call, it can also be used as a

more general long distance location call. Whinnying may also be directed to handlers as a greeting or when food is expected. The whinny is often given at distance and is either replaced by nickers or silence as the handler approaches (A.M. Taylor pers. com.).

The primarily function of the whinny, as a contact call, suggests that the call may be used for individual recognition. It is the most distinctive of the horse calls and also the one that shows the most variation both within and between individuals. Kiley (1972) reports differences in the whinnies of various horse breeds, with finer, lighter varieties producing calls that are less tonal and containing less frequency modulation than the heavier draft breeds. Although fundamental frequency is not generally a good predictor of size within species, the particularly large size variation across domestic horse breeds means that in general smaller horses have higher frequency calls. A detailed study of the temporal and source features of whinnies found that many acoustic parameters could be used to discriminate between the sex, dominance status, size and individual identity but not the age or group affiliation of subjects (Lemasson et al. 2009). Of the 13 parameters measured, 9 were found to be good predictors of individual identity with characteristics of the introductory phase showing the least intra-individual variability. Clear differences in the temporal pattern of whinnies from different individuals can also be seen with, for example, some horses reliably omitting the first phase, or the third phase, or producing a number of separate bouts of low frequency sounds in phase three (Lemasson et al. 2009; L. Proops pers. obs.). See Figure 1.

Interestingly, characteristics of the frequency modulation seen in phase 2 did not show reliable potential for individual identity coding in the Lemasson et al (2009) study. This is perhaps surprising because this bleat-like quality is characteristic of the contact calls of a number of species including sheep, goats and pandas and has been hypothesized to be a salient acoustic method with which to transmit individual identity (Taylor and Reby 2010). In addition, my own preliminary analysis of the acoustic features of whinnies suggested that the speed of frequency modulation was a reliable predictor of individual identity (unpublished data). Further research assessing the full range of acoustic

characteristics of the whinny that have the potential to convey individual identity (including the acoustic characteristics of the filter) would be of benefit. Moreover, many animal vocalisations are individually distinct but playbacks of re-synthesized calls are required to assess the functional salience of these acoustic parameters.

Anecdotal reports do, however, suggest that horses discriminate between familiar and unknown individuals on the basis of their whinnies. When members of a feral band are left behind and subsequently whinny to the group, stallions have been seen to stop the group and wait for the mare to catch up. Calls can be given and responded to when the caller is out of sight and over a quarter of a mile away (Feist and McCullough 1976). Although stallions avoid contact with other harems, it is possible that the whinny of any mare that has become isolated from her group may cause the stallion to investigate the caller as a potential new recruit. However, bachelor bands have also been observed waiting for a group member that has been left behind. This is perhaps more convincing evidence of discrimination based on familiarity because, assuming horses can at least distinguish the sex of the caller, stallions are unlikely to wait for another stallion to approach unless it is a member of their group. Tyler (1972) found that the call of a lost horse generally only elicited a response from members of their own group, implying a degree of discrimination. Stallions also whinny when foals stray too close to another group, at which point the foal returns. Mares may also whinny to recruit the assistance of the stallion when another mare comes too close to her foal (Feist and McCullough 1976).

A few controlled studies of acoustic discrimination have also been reported. As with the nicker, horses will readily respond to playbacks of whinnies. Kiley (1972) tested one horse and found that she responded more readily to calls from stable mates than strangers. However, a small study into mare-foal discrimination found more equivocal results (Wolski et al. 1980). When presented with their own mother/offspring and an unknown mare/foal, both mares and foals non-selectively approached the most vocal of the test pair when visual and olfactory cues were not available. Alien mares were found to call at a much lower rate when they were able to see the foal than when the foal

was out of sight suggesting that identification of the foal did not occur through calls but through visual cues. In playback trials, mares showed some acoustic discrimination by responding more often to the call of their own foal than an unknown foal, with a slight tendency for foals to respond more to their mothers. A recent and more thorough study has shown that domestic horses are able to discriminate between the whinnies of group members, familiar non-group members and strangers, responding more vigorously to group members and least to strangers (Lemasson et al. 2009). This study suggests that horses categorise the calls of others hierarchically, based on the extent of their social bonds.

The Nicker

The nicker is a low/medium amplitude call given with the mouth shut but the nostrils extended and vibrating to give a tremolo. The formants are emphasized and may enable a degree of individual recognition. The pitch is usually around 100Hz and is maintained at the same frequency with little variation. Since the call tends to show low tonality, the fundamental frequency is not very apparent; there is often some fry in this call producing a rattling sound of very low frequency (Kiley, 1972). See Figure 2.
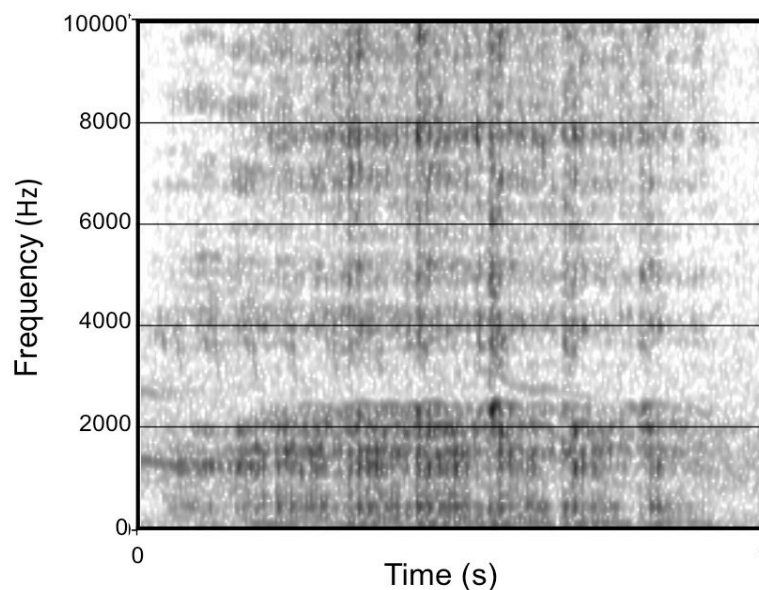
Figure 2: Spectogram of a nicker.

The nicker appears to be a close contact cohesion call given between harem members, mare and foal, and domestic associates (Kiley, 1969, 1972; Tyler, 1972; pers. obs.). It is generally issued when a group member is a short distance away and the caller acts to reduce the distance between them or as the caller approaches a group member as a form of greeting. It is also directed to handlers as a form of greeting particularly when food is expected (pers. obs.). Kiley (1969) performed a series of experiments where horses were shown food that was placed out of their reach. Here horses were more likely to nicker if handlers were in sight or could be heard close by than when they were alone with the food, implying that the call is often directed towards an identified receiver. The sound of a nicker, whether the source is visible or not, is often enough to elicit a response in an animal that is already in a mildly excited state (Kiley, 1972).

The Squeal

The mouth is closed at the onset of this call and then opened with the corners of the mouth drawn back. The call is short and of high amplitude and frequency, often with the fundamental frequency rising during the call (Kiley, 1972). This vocalization occurs during a more specific set of situations than the nicker or whinny. The squeal, described by Kiley (1972) as a defensive greeting, occurs during potentially agonistic interactions and is often given by subordinate animals while greeting a more dominant animal. It is commonly accompanied by a strike with the front legs and a quick withdrawal of the head, or, when an animal is approached by a conspecific from behind, it may be accompanied by a kick or threat to kick (pers. obs.). It is often given by unreceptive mares approached by a stallion and contains information about the reproductive status of the mare (Kim et al. 2010). Horses appear to have individually recognizable squeals and it has been suggested that the squeal is a short, loud adaptation of a whinny issued under high-stress conditions (Kiley, 1972; Browning & Scheifele, 2006). See Figure 3.
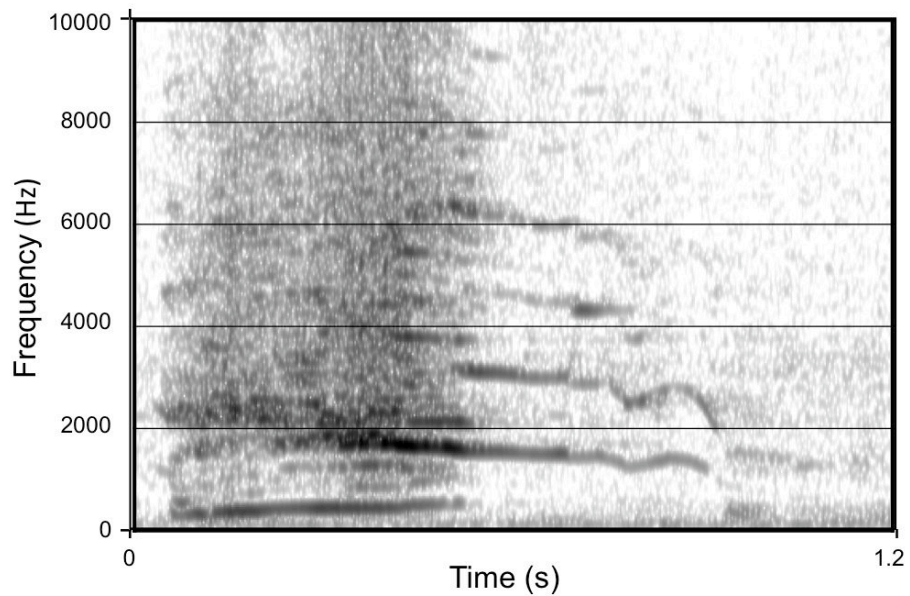
Figure 3: Spectogram of a squeal.

The Snort

The snort is a sound produced by vibration of the nostrils as air is rapidly expelled. The sound is quite high in amplitude and can be heard at a distance of 200 meters. The snort appears to be a natural startle response that has developed into a danger signal used by other group members. Again, this call is only issued in very specific situations, involving fear. The sound is often accompanied by heightened awareness and an increase in muscle tone and either flight/fight or investigative behaviour (Kiley 1972). Detection of this signal by group members produces a corresponding orientation towards the fearful situation and flight/fight response (Tyler 1972). See Figure 4.
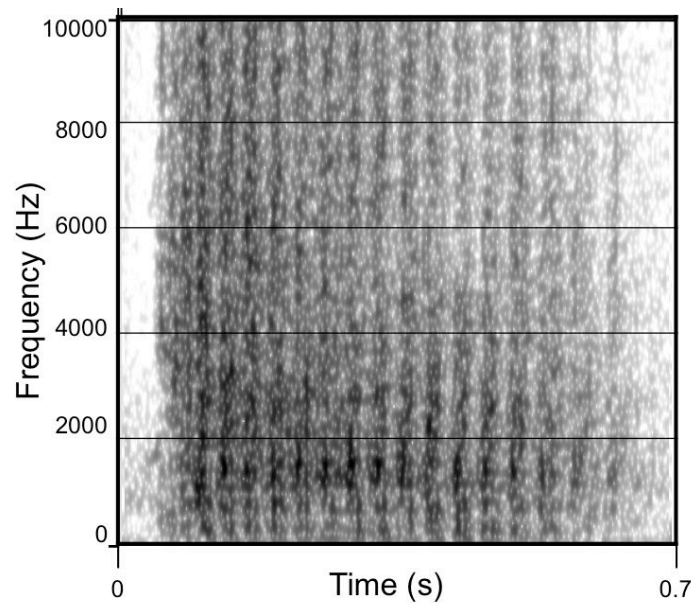
Figure 4: Spectogram of a snort.

Since horses live in fairly stable harems, vocal communication does not appear to play a major role in courtship or the deterrence of competitors; similarly, as grazers, communication is not required to hunt prey or inform group members of a localized patch of food. As social prey animals it seems that one of the main functions of horse communication is to maintain group cohesion and give alarm calls. One aspect of vocalizations that appears particularly important to the horse is the recognition of individuals (Kiley 1972). The whinny, by virtue of its apparent function (long distance contact call) and its physical attributes (relative complexity and individuality), appears to be the call most readily used for this purpose.

The horse-human relationship

In order to understand the horse-human relationship it would be beneficial to understand how horses view people, the extent to which they recognise individuals and, if so, the mechanisms by which this recognition is achieved. It is also of interest to assess the extent and level at which they understand our attempts to communicate in light of their own signalling systems. Understanding these factors would not only further our understanding of comparative

psychology but also have considerable practical and welfare benefits for the management of horses.

Modern horsemanship techniques advocate mimicking, as far as possible, the language of "equus", and in doing so becoming the "lead mare" within a horse group (Roberts 1996). This method presupposes that horses view us as honorary conspecifics, however the extent to which horses view people as affiliates, predators or simply objects in their environment, is unclear. It has been argued that dogs interpret our behaviours in the same way they would the behaviour of other dogs, for example, human play bows are readily interpreted as an invitation to play (Rooney et al. 2001). McGreevy (2009) provides a detailed list of behaviours in the equid ethogram for which corresponding horse-human and human-horse equivalents are possible and those that have no equivalent interactions. The results do suggest that the conspecific model may be appropriate in several contexts because there are many behaviours that horses display to conspecifics and humans but not to predators, such as mutual grooming, head lowering and vocalising. However, interactions with humans certainly differ in important respects to those with conspecifics, and although some of our behaviours towards horses may be comparable to conspecific gestures, such as driving a horse from behind, the duration, context or consistency of the cue may be inappropriate. In addition, there are, of course, no equid equivalents to the communicative cues given while riding. Horses are clearly particularly sensitive to visual communication yet there have been very few studies to date that attempt to determine how horses interpret our postural or communicative cues.

The mechanisms by which horses categorise humans and conspecifics may provide insight into how they perceive their human social partners. As has been mentioned previously, sheep are able to discriminate familiar human faces and although human identity cues are usually processed in the same cortical region as those of dogs (suggesting sheep categorise humans as predators), familiar human faces, associated with positive interactions are processed in the same cortical area as familiar conspecifics (supporting the conspecific model of human-sheep interactions) (Kendrick 2006). To date no comparable research

has been conducted with horses.

Horses tend to show similar reactions to familiar and unfamiliar people and will generalise prior positive or negative experiences with one person or familiar handler to interactions with humans in general (Hausberger and Muller 2002; Henry et al. 2005; Krueger 2007; Lansade and Bouissou 2008; Fureix et al. 2009; Sankey et al. 2010). However, anecdotal evidence suggests that horses are also able to discriminate individuals not just from clothing but also facial features. Arabian horses have been reported to distinguish their owners from similarly dressed people at a distance of over 250m (Waring 2003). Horses have also been found to approach a familiar person and adjust to their direction of attention more than an unfamiliar person during object choice tasks (Krueger et al. 2011).

Controlled studies have shown that horses can learn to discriminate between different classes of people and perhaps between individuals. In a Y maze, two ponies were able to discriminate between an unfamiliar person that had been associated with a positive reward and a familiar handler when both wore the same clothes and scent, but only one of them could discriminate between the unfamiliar rewarder and other unfamiliar people (Koba et al. 2004). In a similar study, the two ponies were found to discriminate between a female handler associated with a reward and a male handler wearing the same clothes and scent but only one of them could discriminate between two female handlers; these discrimination abilities transferred to 2 dimensional full-size images of the handlers (Tanida et al. 2005). In a more extensive study, fourteen out of twenty-five subjects reliably discriminated between an unfamiliar female rewarder and an unfamiliar female non-rewarder when they wore the same clothes. When facial cues were removed subjects' accuracy rates declined and when they were provided with facial cues alone, discrimination was at chance levels (Rossiter 2006). These results suggest that both body shape and facial cues are required for discrimination of individuals, although body cues are more salient.

Interestingly, horses can, given sufficient training, learn to discriminate between the photos of different individuals (even identical twins) based on facial features and then transfer a positive association with one of the photos to a positive response to the actual person (Stone 2009). There is also some anecdotal evidence that horses discriminate between the voice of their handlers and strangers and will preferentially neigh to the sound of their handler (Kiley 1969; L. Proops pers. obs.). However, to my knowledge no formal studies of horse-handler recognition on the basis of voice have been conducted. Assessments of spontaneous discrimination of individual people in any modality have also yet to be conducted.

Section summary

This section outlines the main factors that make the domestic horse an ideal model in which to study social cognition. The evolutionary history of the species coupled with its social organisation and communication systems prompt research into the categorisation of social partners and animal-human relationships. Horses form complex societies in which individuals interact to varying degrees with a large number of conspecifics and there is often a high level of fission-fusion dynamics. Their social organisation involves the development of strong social bonds making it likely that the ability to recognise specific individuals would be a highly adaptive skill. The acute vision of horses coupled with a distinctly individualistic contact call, suggests that cross-modal recognition via auditory and visual cues could be possible. In addition their status as a domestic animal provides the opportunity to investigate the extent to which these recognition skills are flexible in the species they encode. Furthermore, hypotheses concerning the effects of domestication on the ability of animals to read human cues have, to a large extent, been based solely on the abilities of domestic dogs. Horses provide the opportunity to study this skill in a domestic species with arguably the second closest relationship to man but a very different evolutionary background – that of an ungulate prey species. Finally, from a practical point of view, the domestic status of the horse enables

researchers to conduct controlled experiments that would not be possible in the field but continue to be ecologically valid.

AIMS AND THESIS OUTLINE

Aims and research questions

The general aim of this thesis is to explore two areas of horse social cognition that have received very little attention and to draw these findings into the larger framework of the social intelligence hypothesis. These areas are the assessment of horses' ability to categorise social partners, both conspecifics and heterospecifics in the context of social recognition, and the assessment of the extent to which they are capable of understanding communicative cues provided by human partners. How these findings further our knowledge of the ultimate and proximate mechanisms involved in the expression of the above skills across species is also discussed.

More specifically, in this thesis I aim to answer the following questions that relate to these two broad areas of socio-cognitive research:

1) Is an animal – the domestic horse - capable of spontaneous cross-modal individual recognition of conspecifics?
2) Are domestic horses also capable of cross-modal individual recognition of familiar heterospecifics (human handlers)?
3) Is there any evidence of hemispheric specialisation in the processing of cross-modal individual identity cues?

4) To what extent are horses sensitive to human attentional cues?
5) To what extent are horses sensitive to human-given communicative cues that refer to external objects?
6) How do these abilities to read human attentional and communicative cues develop in young horses?

Thesis structure

In the first section of the introduction I outlined the social intelligence hypothesis and provided a definition of social cognition. I then went on to specifically summarise the two fields of social cognition directly relating to my research - the study of how animals classify and discriminate between social partners as part of their natural social behaviour and the study of the extent to which animals are able to comprehend and use human communicative cues. In the second section of the introduction I provided a description of the study species, its evolution and domestication, its social organisation and behavioural repertoire and explained why it is an ideal animal model for the study of social cognition. The research itself will now be presented in the following two sections and is comprised of five research articles. Subsequently I will begin the general discussion of these chapters with a review article explaining what we now know about the social cognition of horses. This will be followed by sections specifically discussing how the findings presented in the main body of the thesis contribute to our understanding of social recognition and human-animal interactions. To conclude I will discuss more generally how my results further our knowledge of comparative social cognition and consider possible avenues for future research.

Outline of articles in this thesis

In the first set of studies (Articles I and II) I investigate the ability of domestic horses to recognise individual social partners. In Article I, I test horses' ability to cross-modally recognise familiar conspecifics using an expectancy violation paradigm. The increased looking time and faster response latencies when the sight of a familiar herd mate was followed by the whinny of a different herd mate compared to when the sight and sound matched, provided the first demonstration that animals are capable of individually recognising conspecifics multi-modally. In the second Article I investigate whether this ability extends to the recognition of familiar human handlers. Using a preferential looking paradigm I found that horses were able to match the sight of a familiar handler to their voice but they did not match a stranger to an unknown voice. These

results demonstrate the potential adaptability and flexibility of cross-modal recognition systems in animals. In addition I found a marked hemispheric lateralisation of discriminatory ability, with horses only being able to perform this task when the congruent handler was standing on their right, suggesting that this ability is governed primarily by mechanisms located in the left hemisphere.

In the second set of Articles (III, IV, V) I explore the other field of social cognition covered in this thesis, the ability of animals to read human given cues. In Article III I assess the extent to which horses are able to use bodily cues to determine whether a person is paying attention to them. In this task, horses showed considerable sensitivity and were able to use not only body orientation but also head direction and eye cues to preferentially approach an attentive person. In Article IV I assess the ability of horses to use human communicative cues to correctly choose a rewarded external location (feed bucket). Here horses were able to use proximal pointing and marker placement cues that potentially provided stimulus enhancement but were unable to use body orientation and gaze cues, suggesting they did not appreciate the referential nature of the cues provided. I then provided the first initial assessment of the ontogeny of these skills by administering these tests to juvenile horses (Article V). Here I found that young horses were less able to use fine body cues to determine the attention of human experimenters than adult horses, although they could use body orientation. In the object choice task young horses performed similarly to adult horses. These results suggest that differing mechanisms and ontogenetic factors are involved in the two tasks.

The final article presented in this thesis provides a review of research into the social cognition of horses (Article VI). Until recently surprisingly little work had been conducted in this area however, in the last five years a growing body of research has developed and a review of this material is warranted. In this article I discuss not only the work presented here but also recent developments in a number of socio-cognitive fields outlined at the beginning of this thesis.

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DISCRIMINATION AND CLASSIFICATION OF SOCIAL PARTNERS

ARTICLE I: CROSS-MODAL INDIVIDUAL RECOGNITION IN DOMESTIC HORSES (*EQUUS CABALLUS*)

Abstract

Individual recognition is considered a complex process and, although it is believed to be widespread across animal taxa, the cognitive mechanisms underlying this ability are poorly understood. An essential feature of individual recognition in humans is that it is cross-modal, allowing the matching of current sensory cues to identity with stored information about that specific individual from other modalities. Here, we use a cross-modal expectancy violation paradigm to provide a clear and systematic demonstration of cross-modal individual recognition in a nonhuman animal: the domestic horse. Subjects watched a herd member being led past them before the individual went out of view, and a call from that or a different associate was played from a loudspeaker positioned close to the point of disappearance. When horses were shown one associate and then the call of a different associate was played, they responded more quickly and looked significantly longer in the direction of the call than when the call matched the herd member just seen, an indication that the incongruent combination violated their expectations. Thus, horses appear to possess a cross-modal representation of known individuals containing unique auditory and visual/olfactory information. Our paradigm could provide a powerful way to study individual recognition across a wide range of species.

Introduction

How animals classify conspecifics provides insights into the social structure of a species and how they perceive their social world (1). Discrimination of kin from nonkin, and of individuals within both of these categories, is proposed to be of major significance in the evolution of social behaviour (2, 3). Individual recognition can be seen as the most fine-grained categorization of conspecifics, and there is considerable interest in discovering the prevalence and complexity of this ability across species. While individual recognition is generally believed to be widespread (4), there is much debate as to what constitutes sound evidence of this ability (5). To demonstrate individual recognition, a paradigm must show that (i) discrimination operates at the level of the individual rather than at a broader level, and (ii) there is a matching of current sensory cues to identity with information stored in memory about that specific individual. Numerous studies to date have provided evidence for some form of social discrimination of auditory stimuli, but how this is achieved remains unclear. It is of considerable interest to establish whether any animal is capable of cross-modal integration of cues to identity, as this would suggest that in addition to the perception and recognition of stimuli in one domain, the brain could integrate such information into some form of higher-order representation that is independent of modality.

A number of species have been shown to make very fine-grained discriminations between different individuals (6–8). For example, in the habituation–dishabituation paradigm, subjects that are habituated to the call of one known individual will dishabituate when presented with the calls of a different known individual. What is unclear from this result is whether discrimination occurs because listeners simply detect an acoustic difference between the two calls or because, on hearing the first call, listeners form a multi-modal percept of a specific individual and then react strongly to the second call not only because of its different acoustic properties, but also because it activates a multi-modal percept of a different individual. Alternative approaches that go some way to addressing this issue have shown subjects to

be capable of associating idiosyncratic cues with certain forms of stored information such as rank category or territory (9–12). However, paradigms to date do not allow researchers to adequately assess whether this form of recognition is cross-modal.

One rigorous way to demonstrate cross-modal individual recognition is to show that an animal associates a signaller's vocalization with other forms of information they have previously acquired in another modality that are uniquely related to that signaller. By presenting a cue to the identity of a familiar associate in one modality and then, once that cue is removed, presenting another familiar cue, either congruous or incongruous in another modality, we can assess whether the presentation of the first cue activates some form of pre-existing multi-modal representation of that individual, creating an ''expectation'' that the subsequent cue will correspond to that associate.

In our study, horses were shown 1 of 2 herd mates who was then led past them and disappeared behind a barrier. After a delay of at least 10 s, the subjects were then played either a call from that associate (congruent trial) or a call from another familiar herd mate (incongruent trial) from a loudspeaker placed close to the point of disappearance. Each of 24 horses participated in a total of four trials: a congruent trial where they saw stimulus horse 1 and heard stimulus horse 1, an incongruent trial where they saw stimulus horse 1 and heard stimulus horse 2, and, the balanced counterparts, a congruent trial where they saw stimulus horse 2 and heard stimulus horse 2 and an incongruent trial where they saw stimulus horse 2 and heard stimulus horse 1 (Fig. 1). Four different pairs of stimulus horses were presented across subjects with six subjects being exposed to each pair. Each subject was presented with a different call exemplar for each associate, so that a total of 48 exemplars were used in the playbacks. The order of trials was counterbalanced across subjects.
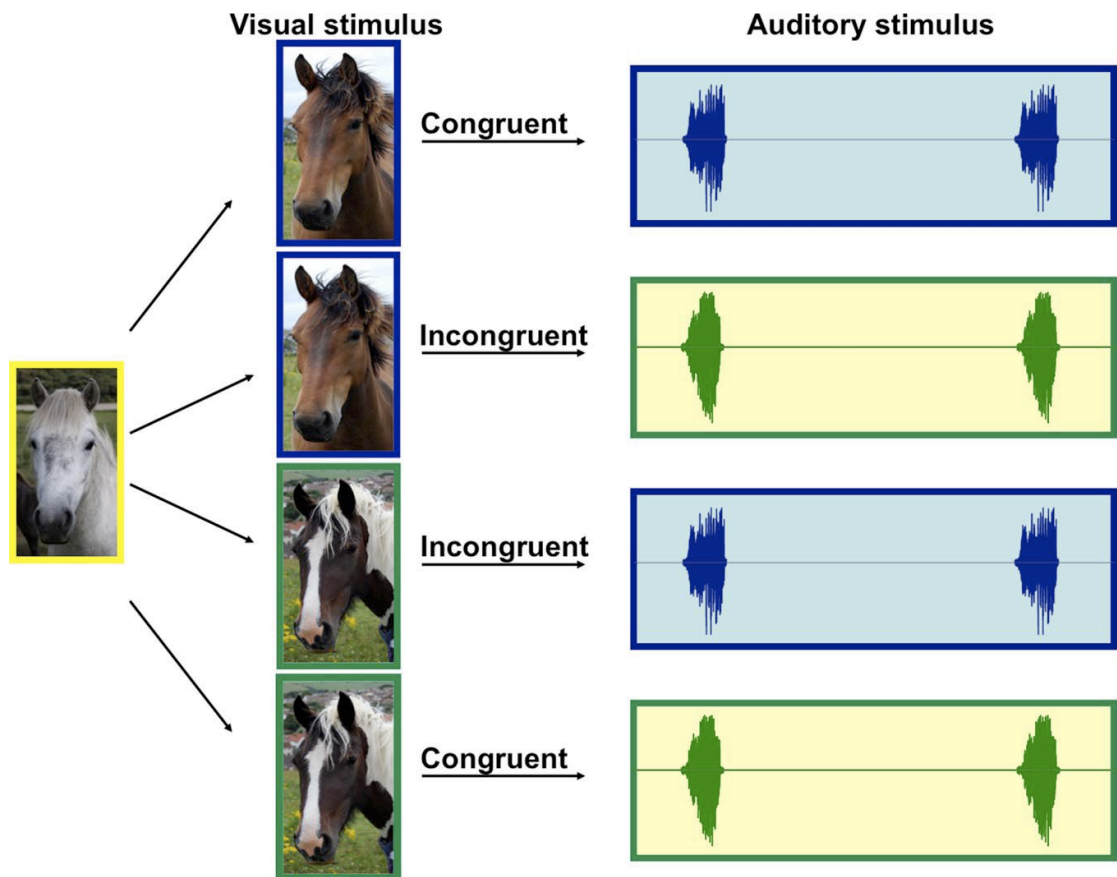
Fig. 1 Diagrammatic representation of the experimental paradigm, as applied to one of our 24 subjects. Each subject receives a balanced set of four trials (detailed in text).

If horses have some form of cross-modal representation of known individuals, and this representation contains unique auditory, visual, and potentially olfactory information, we predicted that the presentation of mismatched cues to identity would violate their expectations. This violation of expectation would be indicated by a faster response time and a longer looking time in the direction of the vocalization during incongruent compared to congruent trials (13).

Results
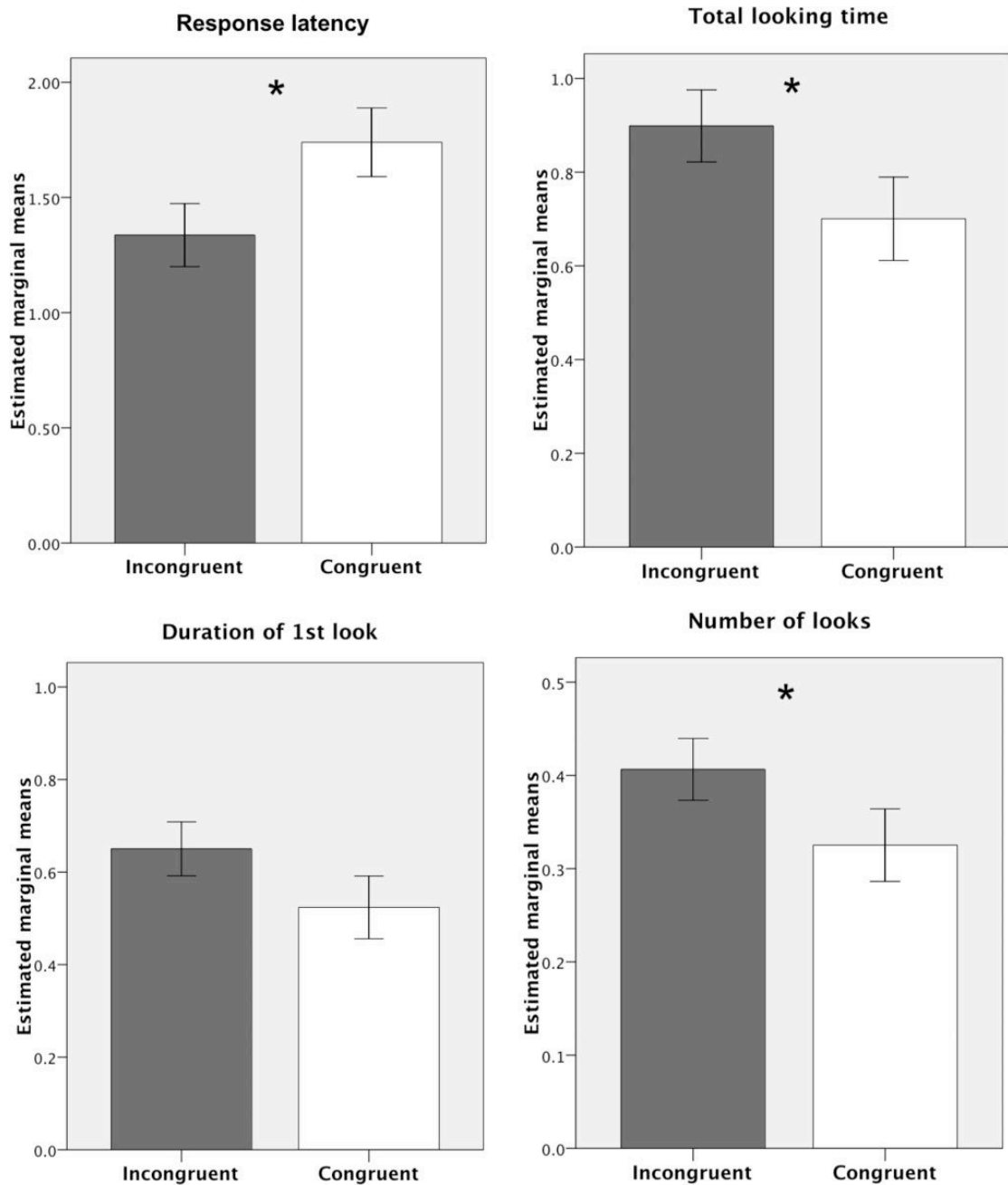
Fig. 2 Estimated marginal means ± SEM for the behavioural responses of subjects during incongruent and congruent trials (* = P < 0.05).

Behavioural responses in the 60 s following the onset of the playbacks are shown in Fig. 2. As predicted, horses responded more quickly to incongruent calls than to congruent calls (response latency: $F_{1,20}$ = 5.136, P = 0.035); they also looked in the direction of the stimulus horse more often and for a longer time in the incongruent trials (number of looks, $F_{1,20}$ = 4.730, P = 0.042; total

looking time, $F_{1,20}$ = 5.208, P = 0.034). There was no significant difference in the duration of the first look (duration of first look: $F_{1,20}$ = 2.802, P = 0.110). These responses did not differ significantly from the first presentation of the calls in trials one and two to the second presentation in trials three and four (response latency, $F_{1, 20}$ = 0.900, P = 0.354; number of looks, $F_{1, 20}$ = 0.019, P = 0.891; total looking time, $F_{1, 20}$ = 0.455, P = 0.508; duration of first look, $F_{1, 20}$ = 0.118, P = 0.735). Neither did subject results differ significantly according to which stimulus horse pair they were presented with (response latency, $F_{3, 20}$ = 1.278, P = 0.350; number of looks, $F_{3, 20}$ = 1.707, P = 0.198; total looking time, $F_{3, 20}$ = 2.098, P = 0.309; duration of first look, $F_{3, 20}$ = 1.996, P = 0.147). There were no significant interactions between the factors. Horses called in response to playbacks during 12 of the 96 trials and calling was not obviously biased toward congruent or incongruent trials (subjects called in 5 congruent compared to 7 incongruent trials).

For each of the four behavioural responses, the scores for the congruent trials were also subtracted from those for the incongruent trials to produce overall recognition ability scores for each subject. Unlike some species, where social knowledge appears to be greater in older animals (7), this research showed no evidence that the ability to recognize the identity of the callers improved with age in an adult population (response latency, r_{22} = -0.015, P = 0.944; total looking time, r_{22} = -0.014, P = 0.947; number of looks, r_{22} = -0.057, P = 0.793; duration of first look, r_{22} = 0.203, P = 0.341). Neither were there any differences in the recognition abilities of male and female horses (response latency, $F_{1, 22}$ = 0.021, P = 0.885; total looking time, $F_{1, 22}$ = 0.153, P = 0.700; number of looks, $F_{1, 22}$ = 0.002, P = 0.967; duration of first look, $F_{1, 22}$ = 0.070, P = 0.794).

Discussion

Overall, horses responded quicker, and looked for a longer time, during trials in which the familiar call heard did not match the familiar horse previously seen, indicating that the incongruent combination violated their expectations. Given that the stimulus horse was out of sight when the vocal cue was heard, our

paradigm requires that some form of multi-modal memory of that individual's characteristics had to be accessed/activated for this result to be obtained. This is the first clear empirical demonstration that in the normal process of identifying social companions of its own species, a nonhuman animal is capable of cross-modal individual recognition.

The ability to transfer information cross-modally was once thought to be unique to humans (14). At the neural level, however, areas responsible for the integration of audiovisual information have now been located in the primate brain. Images of species-specific vocalizations or the vocalizations themselves each produce activation of the auditory cortex and higher-order visual areas and areas of association cortex that contain neurons sensitive to multi-modal information (15–17). This neural circuitry corresponds closely to areas in the human brain that support cross-modal representation of conspecifics and in which differences in activity have been found for presentation of congruent vs. incongruent face–voice pairs (16, 18). Such similarities between human and animal brain function suggest that the possession of higher-order representations that are independent of modality is not unique to humans. Indeed, Ghazanfar (19) considers the neocortex to be essentially multi-sensory in nature, implying that some degree of cross-modal processing is likely to be widespread across mammal taxa.

At the behavioural level, a number of species have recently proved capable of integrating multi-sensory information in a socially relevant way. Nonhuman primates can process audiovisual information cross-modally to match indexical cues (20) and number of vocalizers (21), to match and tally quantity across senses (22) and associate the sound of different call types with images of conspecifics and heterospecifics producing these calls (23–25). Research aimed specifically at investigating the categorization of individuals has shown that hamsters (*Mesocricetus auratus*) are capable of matching multiple scent cues to the same individual (26) and that certain highly enculturated chimps (*Pan troglodytes*) can, through intensive training, learn to associate calls from known individuals with images of those individuals (27–29). Some species have also been shown to spontaneously integrate auditory and visual identity cues

from their one highly familiar human caretaker during interspecific, lab-based trials (30, 31).

Here we demonstrate cross-modal individual recognition of conspecifics in a naturalistic setting by providing evidence that horses possess cross-modal representations that are precise enough to enable discrimination between, and recognition of, two highly familiar associates. The use of two stimulus horses randomly chosen from the herd indicates that our subjects are capable of recognizing the calls of a larger number of familiar individuals, an essential feature of genuine individual recognition (5, 8). If one associate had been slightly more familiar or preferred causing subjects to respond primarily on the basis of differing levels of familiarity, this would have produced biases in favour of the cues of certain individuals that would have been detected in the pattern of the results.

Conducting cross-modal expectancy violation studies in a controlled yet ecologically relevant setting provides the opportunity to re-evaluate and extend the findings of field studies by formally assessing the cognitive processes at work in these situations. Such studies have demonstrated that elephants (*Loxodonta africana*) keep track of the whereabouts of associates by using olfactory cues (32) and that some primates can distinguish between the sound of congruous and incongruous rank interactions and react to acoustic information in ways that suggest they may match calls to specific individuals (9, 33, 34). Our results indicate that cross-modal individual recognition may indeed underpin the complex classification of conspecifics reported and potentially provides a practical and standardized method through which this possibility could be tested directly.

Understanding the extent and nature of abilities to form representations across species is key to understanding the evolution of animal communication and cognition and is of interest to psychologists, neuroscientists, and ethologists. Our demonstration of the spontaneous multi-sensory integration of cues to identity by domestic horses presents a clear parallel to human individual recognition and provides evidence that some nonhuman animals are capable of

processing social information about identity in an integrated and cognitively complex way.

Materials and Methods

Study Animals

Twenty-four horses, 12 from Woodingdean livery yard, Brighton, U.K., and 12 from the Sussex Horse Rescue Trust, Uckfield, East Sussex, U.K., participated in the study. Ages ranged from 3 to 29 years (12.63 ± 1.56) and included 13 gelded males and 11 females. At both sites subjects live outside all year in fairly stable herds of ≈ 30 individuals. The horses from Woodingdean yard are privately owned and are brought in from the herd regularly for feeding; some of them are ridden. The horses at the Sussex Horse Rescue Trust are checked once a day but remain with the herd most of the time. Four horses from each study site were chosen to be "stimulus horses"; these were randomly selected from the horses for which we had recorded a sufficient number of good quality calls. The horses chosen as subjects were unrelated to the stimulus horses, had no known hearing or eyesight problems, and were comfortable with being handled. Only horses that had been part of the herd for at least 6 months could participate to ensure that the subjects would be familiar with the appearance and calls of the stimulus horses. The subjects had not been used in any other studies.

Call Acquisition

We recorded the long distance contact calls (whinnies) of herd members ad libitum. Whinnies are used by both adult and young horses when separated from the group (35–37). All calls were recorded in a situation where the horses had been isolated either from the herd or from a specific herd mate or when the horses were calling to their handler around feeding time. Recordings were

made of both herds between February and September 2007 by using a Sennheisser MKH 816 directional microphone with windshield linked to a Tascam HD-P2 digital audio recorder. Calls were recorded in mono at distances between 1 and 30 m, with a sampling frequency of 48 kHz and a sampling width of 24 bit. Six good-quality recordings, taken on at least two separate occasions, were randomly chosen for each stimulus horse as auditory stimuli. This enabled us to present each subject with a unique call from each stimulus horse to avoid the problem of pseudoreplication (38).

Playback Procedure

Subjects were held by a naive handler on a loose lead rope during trials to prevent them from walking away or approaching their associates. For each subject, one of two possible "stimulus horses" was held for 60 s a few meters in front of them. The stimulus horse was then led behind a barrier and from this point of disappearance, after a delay of at least 10 s, the subjects were played two identical calls with a 15-s interval between each call. Previous work has shown that horses have a short-term spatial memory of <10 s in a delayed response task (39); thus the delay in our recognition task ensured that some form of stored information had to be accessed. The call played was either from the stimulus horse just seen (congruent trial) or from the other stimulus horse (incongruent trial). The subjects were given the four counterbalanced combinations with inter-trial intervals of at least 4 days to prevent habituation (see Fig. 1).

Four pairs of stimulus horses were used, being presented to six subjects each. Presentation of trials and stimulus horses were counterbalanced in that each stimulus horse was used in trials one and two (one congruent, one incongruent) for three subjects and in trials three and four for the other three subjects. The order of congruent and incongruent trials was counterbalanced across subjects with the constraint that the calls of the stimulus horses were presented alternately.

Vocalizations were played from a Liberty Explorer PB- 2500-W powered speaker attached to a Macbook Intel computer. Intensity levels were normalized to 75 dB (± 5 dB) and calls were broadcast at peak pressure level of 98 dB 1 m from the source (taken as the average output volume of subjects recorded previously). Responses were recorded by using a Sony digital handycam DCR-TRV19E video recorder. Handlers were naive to the identity of the callers. They were asked to hold the horses in front of the video camera on as loose a rope as possible, allowing the horses to graze and move around freely on the rope. The handlers remained still, looking at the ground and did not interact with the subjects.

Behavioural and Statistical Analysis of Responses

Videotapes were converted to .mov files and analyzed frame by frame (frame, 0.04 s) on a Mac G4 powerbook, by using Gamebreaker 5.1 video analysis software (40). The total time subjects spent looking in the direction of the speaker in the 60 s following the onset of the playbacks was recorded. The onset of the look was defined as the frame at which the horse's head began to move toward the speaker, having previously been held in another position. A fixed look toward the speaker was then given and the end of the look was taken to be the frame at which the horse began to move his head in a direction away from the speaker. A look was defined as being in the direction of the call if the horse's nose was facing a point within 45° to the left or the right of the speaker. The duration of the first look toward the speaker, the total number of looks, and the total looking time were recorded. Latency to respond to the call was also measured and defined as the number of seconds between the onset of the call and the beginning of the first look in the direction of the speaker. For subjects that did not respond, a maximum time of 60 s was assigned.

The videos were coded blind in a random order. Twenty videos (20.8%) were scored by a second coder, providing an inter-observer reliability of 0.968 ($P < 0.0001$) for total looking time, 0.992 ($P < 0.0001$) for response latency, 0.907 ($P < 0.0001$) for number of looks, and 0.995 ($P < 0.0001$) for duration of first look,

measured by Spearman's rho correlation. The distributions of scores for total looking time, duration of first looks, and number of looks were positively skewed and so were $\log_{10}$ transformed to normalize the data. The distribution of the response latency scores was bimodal and so a fourth root transformation was performed. Results were analyzed by using

2 x 2 x 4 mixed-factor ANOVAs with condition (congruent/incongruent) and trial (trials 1 and 2 using stimulus horse 1/trials 3 and 4 using stimulus horse 2) as within-subject factors and stimulus pair (which pair of stimulus horses were presented) as a between-subjects factor. Each dependent variable (total look duration, duration of first look, number of looks, and response latency) was analyzed in a separate ANOVA. The effect of age and sex was investigated by subtracting the congruent responses from the incongruent responses and adding up the total for each subject to obtain a measurement of the magnitude of difference in responding to congruent and incongruent trials for each subject, i.e., (incongruent trial 1 - congruent trial 1) + (incongruent trial 2 - congruent trial 2). A score of 0 would indicate no difference in the behaviour of a subject across the trial types, a positive score would indicate a larger response to the incongruent trials, and a negative score would indicate a greater response to the congruent trials. This measurement of the degree of recognition by each subject was calculated for the four behavioural responses and was correlated with age of subjects, by using Pearson's correlation coefficient. The recognition score for male and female subjects was compared by using a one-way ANOVA.

Acknowledgements

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ARTICLE II: CROSS-MODAL RECOGNITION OF HUMANS BY DOMESTIC HORSES (*EQUUS CABALLUS*) SHOWS HEMISPHERIC SPECIALISATION

(Proops, L. & McComb, K. 2011*.* In the style of *BMC Biology)*

Abstract

Background: The ability to recognise specific individuals is central to performing complex social interactions. The recent evidence that domestic horses and some primates are capable of cross-modal individual recognition indicates how sophisticated these abilities can be and suggests such skills have a long phylogenetic history. In our study we investigate how adaptable this recognition system is by assessing whether cross-modal recognition in horses extends to identifying familiar people. In addition we provide the first insights into the hemispheric specialisation at work in animals during the natural assimilation and activation of cross-modal social information.

Results: A preferential looking paradigm was employed in which horses were presented with two people and playbacks of their voices to determine if they were able to spontaneously match the voice to the person. When presented with a stranger and a familiar handler, horses could match the familiar voice to the familiar person but did not match the unknown voice to the stranger. When presented with two highly familiar handlers in a more demanding cross-modal recognition task, subjects were able to match the specific familiar person to the correct familiar voice.

Conclusions: These results demonstrate that horses' ability to cross-modally recognise individuals is highly plastic and can be employed to recognise not only familiar conspecifics but also morphologically very different heterospecific individuals. Moreover, horses were better at performing the matching task when the person was standing to their right, indicating a left hemisphere bias in discriminatory ability. We discuss what possible functional cerebral asymmetries may give rise to this lateralisation.

Background

Being able to identify individual social partners is central to developing sophisticated social relationships. A key element of individual recognition in humans is that it is cross-modal, allowing the matching of the sight of a person to their voice. Cross-modal matching was once thought to be unique to humans [1], and although individual recognition is believed to be widespread [2], it has been hard to prove conclusively in animals because this requires a demonstration not only that discrimination between identity cues occurs at the level of the individual but also that current sensory cues match stored information about that specific individual. In addition, if animals are capable of combining cues to an individual's identity cross-modally, this suggests these cues are ultimately stored in some form of higher-order representation that is independent of modality. An expectancy violation paradigm has recently been used to demonstrate that domestic horses are indeed capable of spontaneous cross-modal individual recognition of conspecifics, indicating that the ability is likely to have a long phylogenetic history [3]. The ability to match the sight of familiar individuals with their voice, without explicit training, has also since been demonstrated in nonhuman primates [4, 5].

For domestic animals, humans also represent significant social partners. Domestic dogs have been shown to match the image of a single familiar person to their voice but in a design where matching of familiar stimuli rather than activation of a representation of a specific individual might have occurred [6]. Domestic horses are capable of discriminating between different human faces and have been shown to discriminate between familiar and unfamiliar people [7, 8] but genuine cross-modal individual recognition of heterospecifics has yet to be demonstrated outside of the primate taxa [4]. The prevalence of this ability across different species therefore remains unknown. It also remains possible that the relatively similar physical features of humans and primates in some way facilitate recognition of humans by primates [9]. Thus one aim of this study is to assess whether a non-primate species with a very different morphology but a close relationship to humans, is capable of cross-modal recognition of a range of familiar people. This would suggest not only that cross-modal individual

recognition is widespread among mammals but also that is it highly plastic in the morphology of individuals that it can code.

Moreover, in our study we also provide the first investigation into cerebral functional asymmetries associated with the ability to spontaneously recognise individuals cross-modally. A general explanation of the roles of the different hemispheres suggests that the left hemisphere provides focussed attention and is involved in top-down processing, controlling well established patterns of behaviour as well as approach responses and the categorisation of familiar stimuli whereas the right hemisphere is more under bottom-up control and is central to the processing of novel, potentially threatening stimuli and producing corresponding escape behaviour [10-12].

The general left hemisphere specialisation for language in humans has parallels in a widespread bias towards the left hemisphere for the production and processing of conspecific calls in other species [10, 11, 13] although some exceptions have been reported [14, 15]. In contrast heterospecific calls and non-biological sounds tend to either be processed by the right hemisphere [16-20] or do not appear to be lateralised [15, 20-23]. In the visual domain both conspecifics and heterospecifics appear to be preferentially viewed with the left eye although the mechanisms involved are different, with the response to heterospecifics mainly associated with predator detection and responses to conspecifics being due to the activation of areas specialised in the identification of members of the same species [10, 11, 24]. However, familiarity with specific individuals has been shown to reduce or eliminate this right hemisphere bias [25, 26]. When multi-sensory integration of voice-face information occurs, results tend to show a synchronisation of activation between face and voice selective areas, often with activation of additional cortical areas that may be the location of semantic information about particular individuals (so called "person identity nodes") [27]. Specific right hemispheric activation of these areas has been reported by some studies but assessment of the corresponding behavioural asymmetries that may occur during these tasks has not been made [28-30]. With the vast array of often seemingly contradictory laterality studies, it is hard to extract the relevant features of a task and predict a priori whether a

particular hemispheric dominance will be seen in social recognition experiments.

Our study therefore not only provides the first assessment of heterospecific cross-modal individual recognition outside of primate species but also provides the first insights into the neural processes at work during the natural assimilation and activation of cross-modal social information in animals. The domestic horse is an ideal animal model for this research because it has a complex social organisation and close relationship to man, making individual recognition of humans a highly functional ability. We employed a preferential looking paradigm to determine if horses could match playbacks of human voices to the sight of those specific people. Two people stood either side of a loudspeaker from which the voices of each person (giving 2 renditions of the subject's name) were played with an interval of 15 seconds between presentations of the different voices (Fig. 1). Horses stood facing the people on the centre line and their responses to the congruent and incongruent person were recorded. In Experiment 1, we tested 32 horses for the ability to use cross-modal information in a basic task involving discrimination of known individuals from strangers. In Experiment 2, 40 horses were tested for whether they could perform the more complex task of cross-modal individual recognition by virtue of presenting them with a choice between two different familiar humans (10 pairs of handlers were presented to 4 subjects each). To ensure that the humans were not inadvertently cuing the horses, a control was included in which handlers listened to white noise on small headphones to prevent them hearing the playback itself. If horses are capable of cross-modal discrimination of familiar from unfamiliar people and recognition of familiar handlers, we predicted they would be quicker to look and look for longer at the person that matched the voice just heard. Analyses of side preferences and success at discrimination in relation to the side on which the matched person was standing were conducted to examine whether horses showed any behavioural asymmetry in orienting response and in recognition/discrimination ability.
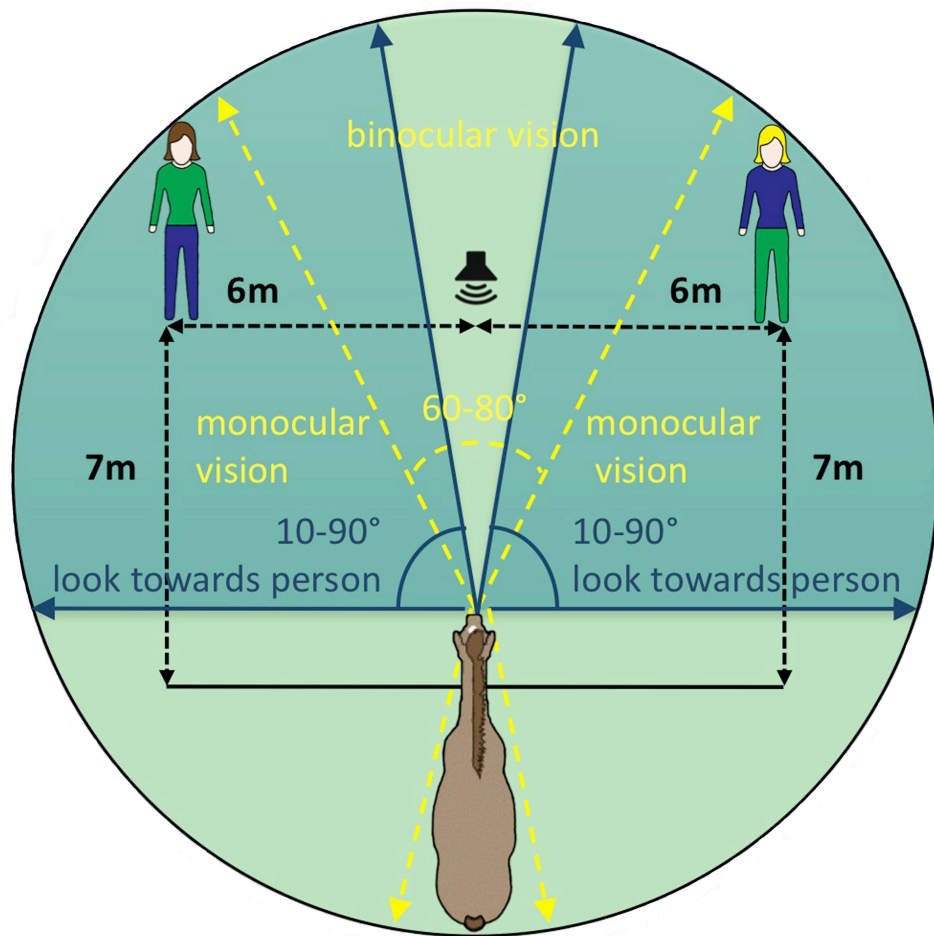
Fig. 1. Diagram showing the experimental set up and subject head orientations defined as looks towards each person, the speaker and elsewhere in relation to the binocular and monocular fields of the horse.

Results and Discussion

Experiment 1: Cross-modal discrimination of familiar human handlers from strangers.

As predicted horses were faster to look and spent more time overall looking at the congruent compared to the incongruent person (Response latency: $F_{1, 31} = 5.72$, $P = 0.023$; Looking time: $F_{1, 31} = 10.82$, $P = 0.003$). However, for total looking time there were also a significant interaction between congruency and whether the voice heard was the owner or the stranger, suggesting that the time spent looking at the congruent and incongruent person was different depending

on whether the voice was the owner's or the stranger's (Looking time: $F_{1,\ 31}$= 5.27, P = 0.029). This was also supported by a parallel trend in response latency that bordered on significance (Response latency: $F_{1,\ 31}$ = 4.058, P = 0.053).

When the results are broken down further it emerges that although the horses were faster to look and spent significantly more time looking at the owner when they heard the owner's voice (Response latency: t_{31} = -3.10, P < 0.01; Looking time: t_{31} = 3.77, P < 0.005) they did not respond faster and look for longer at the stranger when they heard the stranger's voice (Response latency: t_{31} = -0.13, $N.S.$; Looking time: t_{31} = 0.62, $N.S.$). In addition horses tended to look more often at the owner compared to the stranger when they heard the owner's voice (z = 1.94, P = 0.052) but did not look more often at the stranger compared to the owner when they heard the stranger's voice (z = 0.66, P = 0.51). We therefore excluded the trials in which the stranger's voice was played from further analysis (Fig. 2A).

Within the responses to the owners' calls we found that subjects were faster to respond, looked for longer and more often at the owner compared to the stranger when the owner was standing on the right side of the subject (Response latency: t_{17} = -3.27, P = 0.005; Looking time: t_{17} = 3.19, P = 0.005; Number of looks: z = 2.63, P = 0.023). However, when the owner was standing on the left side of the subject, they did not look more quickly, for longer or more often at the owner compared to the stranger, although the difference in total looking time did border on significance (Response latency: t_{17} = -1.03, P = 0.32; Looking time: t_{17} = 2.05, P = 0.061; Number of looks: z = 0.37 P =0.71) indicating that horses were considerably poorer at making the match when the owner was not standing on the right side (Fig. 2B). There were no significant differences in the direction of the first look (owner: 19 right turns, 10 left turns and 3 no responses; N = 29, K = 19, P = 0.14; stranger: 12 right turns, 14 left turns and 6 no responses; N = 26, K = 12, P = 0.85), or in total number of looks given in each direction (owner: 30 right turns, 20 left turns; N = 50, K = 30, P = 0.20; stranger: 21 right turns, 21 left turns; N = 42, K = 21, P > 0.99).
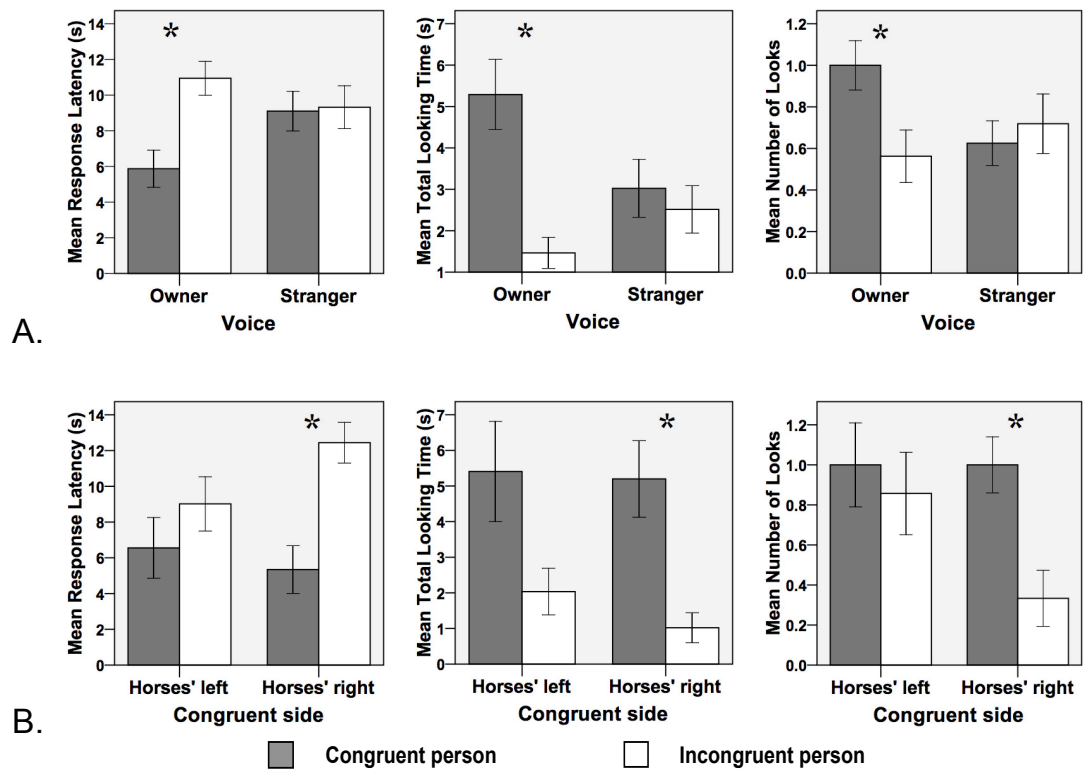
Fig. 2. Experiment 1: Cross-modal discrimination of human handlers and strangers. **(**A) Means ± SEM for the behavioural responses of subjects to the matched (congruent) versus the mismatched (incongruent) person during the trials in which the owner and the stranger were heard (*N* = 128)**.** * = *P* < 0.05. (B) Means ± SEM for the behavioural responses of subjects to the owner's voice during the trials in which the owner was on the right side of the horse versus when they were on the left (*N* = 64). * = *P* < 0.05.

Experiment 2: Cross-modal individual recognition of human handlers.

Subjects were faster to look, looked more often and for longer at the familiar person whose voice they had just heard compared to the familiar person whose voice they had not heard (Response latency: $F_{1, 312}$ = 6.815, *P* = 0.009; Looking time: $F_{1, 312}$= 11.164, *P* = 0.001 Number of looks: $F_{1, 234}$ = 7.801, *P* = 0.006; Fig. 3A).
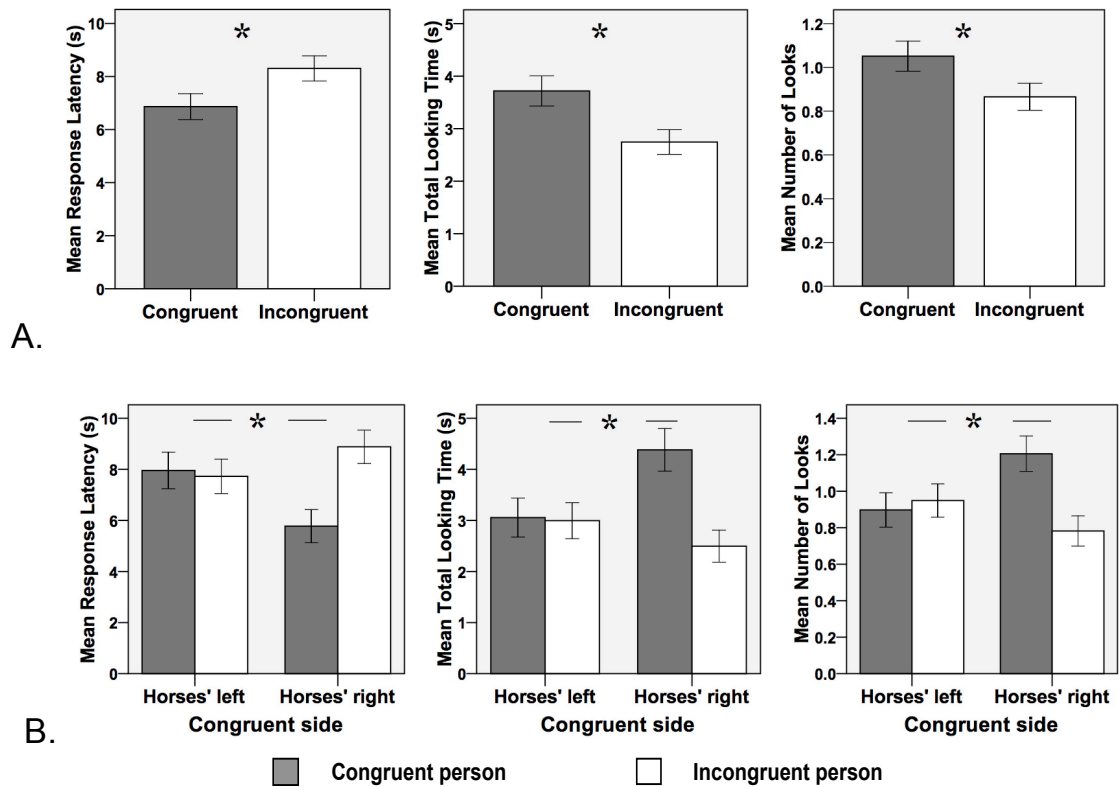
Fig. 3. Experiment 2: Cross-modal individual recognition of familiar human handlers. (A) Means ± SEM for the behavioural responses of subjects to the matched (congruent) versus the mismatched (incongruent) person (N = 312). * = P < 0.05. (B) Means ± SEM for the behavioural responses of subjects during trials in which the congruent person was on the right side of the horse versus when they were on the left (N = 312). * = P < 0.05.

Across the three behavioural measures (response latency, looking time and number of looks), models containing the predictor variables sex and side on which the congruent person stood best explained the data. Specifically, horses found it easier to correctly match the handler to their voice if they were standing on their right side (Fig. 3B) and female subjects were better at recognising their handlers (Response latency: Congruency*side $F_{1, 312}$ = 6.593, P = 0.011, Congruency*sex $F_{1, 312}$ = 3.942, P = 0.048; Looking time: Congruency*side $F_{1, 312}$ = 6.446, P = 0.012, Congruency*sex $F_{1, 312}$ = 9.348, P = 0.002; Number of looks: Congruency*side $F_{1, 234}$ = 7.937, P = 0.005, Congruency*sex $F_{1,234}$ = 7.801, P = 0.006). Additionally, there was a main effect of age on response latency with horses from the youngest age group (0-5yrs) responding faster to

the playbacks ($F_{4, 312}$ = 3.408, P = 0.010). There was also a main effect of trial part/playback on number of looks, with subjects giving more looks overall in response to the first voice heard in a trial compared to the second voice ($F_{1, 234}$ = 4.699; P = 0.031). Measures of familiarity, trial order and number of handlers did not significantly explain variance in recognition ability and were not included in the final models.

There were no significant differences in the direction the subjects first looked when they heard a familiar handler's voice (81 right turns, 61 left turns and 14 no responses; N = 142, K = 81, P = 0.11). There was however, a significant difference in the total number of looks given in each direction, with subjects looking right more often than left (168 right turns, 131 left turns; N = 299, K = 168, P = 0.037).

Discussion

In our first experiment, subjects looked faster, for longer and more often at their owner when they heard their owner's voice than when they heard a stranger's voice. In contrast, they did not look for longer at the stranger when they heard the unfamiliar voice. Thus subjects were able to match a familiar voice with a familiar person but did not match an unfamiliar voice to an unfamiliar person, although whether this reflects an inability to infer that an unknown voice comes from an unknown individual or they are not motivated to respond to a stranger calling their name, is unclear. In the second experiment subjects proved able to match a specific familiar voice to a specific familiar human handler. This indicates that the sight of the handler activated a multi-modal memory of that specific individual, allowing subjects to match the sight of that particular person with the sound of their voice. This is the first demonstration that an animal outside of the primates is capable of spontaneous cross-modal individual recognition of familiar heterospecifics. Furthermore, the ecologically valid methodology and the large number of handlers pairs presented suggest that horses utilise this recognition strategy naturally to identify numerous individual people in their day-to-day lives.

Our results indicate that individual recognition abilities in animals can also be highly versatile, encoding individuals that are morphologically distinct from the species itself. In humans, auditory, visual and cross-modal perceptual narrowing occurs over the course of the first year of life [31]. Animals also show a specialised ability to discriminate conspecific faces [32] but, like humans, animals with significant exposure to heterospecifics do demonstrate improved discriminatory abilities [33-35] and appear to process heterospecific identity information similarly to that of conspecifics [36, 37]. Thus it is clear that familiarity with heterospecifics can to some extent enable identity information from other species to be processed in similar ways to that of conspecific individuals. What the current research and that of Silwa et al [4] shows is that this adaptability can extend to the most complex of social recognition tasks – that of cross-modal individual recognition.

Female horses were significantly better at recognising particular handlers, although there were no sex differences in performance during the easier task of discriminating between familiar and unfamiliar people. In the wild, horse social organisation has been described as matriarchal and females form close social bonds, the quality of which has been shown to directly impact on the fitness of individuals [38]. Thus the importance of forming good social relationships and of recognition of offspring may lead to enhanced socio-cognitive skills in females, although why this was not evident in previous research into the cross-modal recognition of conspecifics is unclear (5). It is interesting, however, that female horses have also proved better able to gauge the attentional state of humans [39].

Overall horses were significantly better at matching the familiar person to the sound of their voice when the correct person stood on their right side, with this asymmetry being more pronounced in the second experiment. Subjects also showed a trend towards preferring to orient to the right when the playbacks were heard. Although horses were free to look at the people with both eyes prior to and during the playback of vocalisations, the position of the people lay in their monocular field when subjects were facing forwards (Fig. 1). We

therefore interpret the above findings as the horses having been better at identifying the person initially with the right eye. There are a number of possible explanations as to why the left hemisphere could be central to cross-modal individual recognition in horses.

Although visual and cross-modal studies matching voice-face stimuli in humans and primates have tended to reveal an overall right hemisphere bias in processing, right hemispheric activation is followed by subsequent increases in left hemispheric activation [13, 24, 27, 40, 41]. It has been suggested that the right hemisphere is responsible for the initial processing of identity information and the assessment of novelty versus familiarity whereas the left hemisphere may be involved in the more top-down retrieval of memories and details associated with specific individuals [42]. Crucially, our study is different from most other research into hemispheric specialisation in that it involves the retrieval of information about genuine social partners associated with long-term relationships rather than responding to arbitrary voice-face pairs learnt in lab-based studies. In addition, the familiarity of animals, including horses, to specific humans or humans in general has been shown to reduce the right hemispheric bias in viewing people [25, 26, 43]. There has been only one study of auditory lateralisation in horses to date, which showed a left hemisphere preference for the processing of familiar conspecific non-group members but not for strangers or group members [44].

It is widely accepted that the left hemisphere is involved in the categorisation of familiar objects other than faces and is implicated in general cross-modal matching to sample [11, 12, 24]. In our study horses were presented with the sight of the whole body rather than just a face and may thus have been primarily using other attributes to assign identity. Such a task would require the use of mental templates based on previous experience and the implementation of established strategies of behaviour that are governed by the left hemisphere, as shown in both monkeys and dolphins [45, 46]. The task given to the dolphins is particularly relevant here: subjects were trained to associate audio stimuli, including known signature whistles, human voices and tones with visual objects, including videos of dolphins and people. Subjects showed no strong eye

preference but were significantly better at matching the audio-visual stimuli across all categories if objects were viewed by the right eye.

The left hemisphere has correspondingly been implicated in the direction of focussed attention, attending preferentially to aspects of a stimulus that are invariant and hence relevant to categorisation, and also controls responses to stimuli that elicit strong approach behaviour. In contrast, the right hemisphere is more subject to distraction by irrelevant stimuli due to its function in detecting novelty and controls avoidance of negative stimuli [10-12, 47]. Thus it is possible that the right hemisphere was less equipped to direct sufficient attention to perform the discrimination when the congruent person was on the left side. This effect could have been more pronounced in the second, more demanding experiment because the presence of an incongruent familiar person in Experiment 2 may also have produced a corresponding desire to approach when viewed with the left hemisphere which would not have been the case when viewing the incongruent stranger person in Experiment 1.

Conclusions

These results demonstrate that domestic horses are capable of cross-modal individual recognition of familiar human handlers. This is the first evidence that an animal other than a primate is capable of cross-modal recognition of heterospecifics and suggests that such an ability is likely to be widespread. It further demonstrates the adaptability of recognition systems – particularly because humans and horses are phylogenetically and morphologically so different. In addition, we also provide the first report of strong hemispheric asymmetry during the processing of cross-modal identity information in a naturalistic setting. By determining the prevalence and plasticity of individual recognition systems and providing insights into the hemispheric specialisations on which these mechanisms are based across species, we broaden our understanding of the evolutionary history and neural bases of conceptual knowledge and social cognition.

Methods

Study animals.

All subjects had been owned/cared for by their female handlers for at least 6 months prior to the study. Subjects were turned out in fields during the day and were brought in regularly for feeding and riding, some were brought in overnight. Subjects were naive to the experimental set up and participated in only one of the following experiments. In experiment 1, a total of 32 horses were recruited from 5 private livery yards in Norfolk and Sussex, UK. Ages ranged from 1.6 - 31 years (X±SE =12.83 ± 1.47) and included 14 gelded males and 18 mares. In experiment 2, a total of 40 horses were recruited from 9 private livery yards and riding schools in Kent and Sussex, UK. 10 pairs of handlers were recruited, each sharing the care of four of the subjects. One horse was sold during the study, leaving a total of 39 subjects in the final analysis. Ages ranged from 2-25 years (X±SE = 13.97 ± 0.94) and included 23 gelded males, 1 stallion and 15 mares.

Call acquisition.

Handlers were recorded calling the names of their horses in a stern voice. Handlers participating in experiment 1 were also recorded calling the name of an unfamiliar subject from another livery yard. In this way the voices of handlers were used both as the familiar voice for their own horse and as the voice of a stranger for a different subject. Recordings were made using a Sennheisser 416 directional microphone linked to a Tascam HD-P2 digital audio recorder. Calls were recorded in mono at a distance of 1m, with a 24-bit resolution and a sampling frequency of 48 kHz. Recordings were transferred to a 2 GHz Intel MacBook and the first two good quality recordings from each handler for each horse were chosen as playback stimuli. The intensity levels were standardised to 75dB (±5dB) using Praat software v.5.0.38 and playbacks were assembled using Audacity software v.1.3.6.

Playback procedure.

A preferential looking paradigm was employed (see Fig. 1 for details of experimental set-up). Experiments were carried out in a familiar paddock or school during February 2009 - July 2010. Subjects were held on a loose lead rope 7m in front of a speaker while two people stood 6m to the left and right of the speaker facing the horse. In Experiment 1 the two people were a familiar handler and a person unknown to the subject. In Experiment 2 the people were two highly familiar handlers. Subjects were played two calls by one person (with a 1 second interval) and then, after 15 seconds of silence, two calls from the second person were played. Calls were played from a Liberty Explorer PB-2500-W powered speaker attached by a long audio lead to an ipod. An experimenter out of sight of the test area operated the ipod. The speaker was disguised by either vegetation or show jumping wings. The order of the voices and the side that the people stood on were counterbalanced across trials. The person holding the subjects remained still, looking forward and did not interact with the horses. In Experiment 1 subjects were given one trial in which the horses heard the two calls of each person once. In Experiment 2 subjects were given two trials separated by at least one week. The order in which the voices were played and the sides on which the handlers stood were counterbalanced across these trials. In order to ensure that the people participating in the study were not giving any unintentional cues when they heard the playback of their voices, 16 subjects in experiment 2 received one trial in which the handlers wore small earpiece headphones and listened to white noise from handheld MP3 players and one trial without headphones. This white nose masked the sound of the playbacks. The responses of the horses to the trials with and without the headphones were compared to ensure that the horses' recognition ability was not significantly improved when the handlers could also hear the playbacks. Responses were recorded on a Sony digital handycam DCR-TRV19E.

Ethics statement.

The methods employed in this study were observational and non-invasive and involved a procedure that was similar to interactions the subjects would encounter in their daily lives. As such this study did not require a licence under the United Kingdom Home Office regulations concerning animal research and welfare. This study complied with the University of Sussex regulations on the use of animals and was approved by the School of Psychology ethics committee.

Behavioural and statistical analysis.

Responses were converted to mp4 files and analysed frame by frame (frame = 0.04s) on an Intel Macbook using Gamebreaker video analysis software v.7.4.1. A look towards one of the people was recorded as commencing on the frame at which the horse's head began to move toward them having previously been held in another position. A fixed look toward the person was then given and the end of the look was taken to be the frame at which the horse began to move his head towards an alternative direction. The total amount of time spent looking at the each of the people, the speaker and elsewhere was recorded. Horses have laterally placed eyes with a small (60-80°) binocular field of vision and almost complete (80-90%) decussation of the optic nerves, suggesting that behavioural asymmetries reflect asymmetries in hemispheric activation [48, 49]. A look was thus defined as being at either of the people if the horse's nose was between 10 and 90° from the centre line and was recorded as being in the direction of the speaker if the horse's nose was facing a point within 10° to the left or the right of the speaker; a look was recorded as "elsewhere" if it was over 90° from the centre point (Fig. 1). Response latencies, the total amount of looking time and the number of looks given to the congruent and incongruent person were recorded as DVs. For subjects that did not look at one (or both) of the people during a playback, a maximum time of 15s was assigned as the response latency towards that particular individual. The videos were coded blind in random order by LP. For experiment 1 the total looking time and number of

looks for 22/32 subjects (69%) were scored by a second coder providing inter-observer reliabilities of 0.704 ($P < 0.0001$) and 0.703 ($P < 0.0001$) respectively. For experiment 2, the videos of 23/39 subjects (59%) were second coded, providing an inter-observer reliability of 0.674 ($P < 0.0001$) for response latency, 0.723 ($P < 0.0001$) for total looking time and 0.627 ($P < 0.0001$) for number of looks (measured by Spearman's rho correlation). All statistical analyses were conducted using SPSS v. 17 for Mac OSX.

<u>Experiment 1.</u> For the DVs of response latency and total looking time, initial 2x2 repeated measures ANOVAs were conducted with congruency (congruent/incongruent) and person heard (owner/stranger) as within-subject factors. Additional repeated measures t-tests (adjusted using the Bonferonni correction) were performed to assess the differences in latency and looking time towards the incongruent and congruent person for the owner's voice and the stranger's voice separately. The DV number of looks was not considered to be a continuous variable due to the limited distribution of responses (range 0-2) thus non-parametric Wilcoxon signed ranks tests were used to compare the differences in number of looks given to the incongruent and congruent person for the owner's voice and the stranger's voice separately. The responses to the owner's voice were then divided into those trials where the owners stood on the left of the subject and those in which they stood on the right. Individual t tests were then performed on the response latency and total time data for the two groups to assess the effects of side on performance. The effect of side on number of looks given was also analysed using Wilcoxon signed ranks tests.

<u>Experiment 2.</u> Due to the larger sample size and multiple trial protocol employed in experiment 2, each DV could be analysed in an individual linear mixed model (with a scaled identity covariance structure, using a maximum likelihood estimation). The fit of potential models was determined using Akaike's Information Criterion corrected for small samples (AICc) and ranked using ΔAICc to determine the best fit model. All factors listed below were included in a global model and factors with little or no predictive value were systematically removed to produce the final, best model.

In these models handlers' voice was nested within subject as a random factor. The main effect assessed was congruency i.e. were there any significant differences in the response latency, number of looks and total time spent looking at the matched and mismatched person. The following potential predictor variables were also included as fixed factors: horse sex, age (grouped variable (GV)), side on which handler stood, number of handlers, number of years the horse had known each handler (GV), estimated number of hours a day spent with each handler (GV) and total exposure time (GV; calculated by the number of hours a day spent with the person X years known). Order effects were assessed by the repeated measure of trial order (1 and 2) with playback (1 and 2) nested within trial. To assess the effect of these additional potential predictor variables on the ability to distinguish between congruent and incongruent people each factor was included as an interaction variable with congruency (factor*congruency).

Within both experiments, the direction of the initial look and the total number of times subjects looked in each direction when they heard the two voices were compared using two-tailed binomial probability tests to determine if there was a group level orienting asymmetry when hearing familiar or unfamiliar voices. To ensure that handlers were not unintentionally cuing the horses during the trials, the recognition ability of the subjects during experiment two when handlers could hear the playbacks and when they could not, were compared using a 2X2X2 repeated measures ANOVA with playback (voice1/voice2), congruency (congruent/incongruent) and trial type (with headphones/without headphones) as within subject factors. No significant differences between the trials in which handlers could hear the playbacks and those in which they could not were found (Response latency: $F_{1,15}$ = 0.663, P = 0.43; Total looking time: $F_{1,15}$ = 2.391, P = 0.14; Number of looks: $F_{1,15}$ = 1.901, P = 0.19) and the data were therefore combined in all subsequent analyses.

Acknowledgments

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OBTAINING INFORMATION FROM HUMAN SOCIAL PARTNERS

"They [horses] have always understood a great deal more than they let on. It is difficult to be sat on all day, every day, by some other creature, without forming an opinion about them. On the other hand, it is perfectly possible to sit all day, every day, on top of another creature and not have the slightest thought about them whatsoever."

Douglas Adams (1987) Dirk Gently's holistic detective agency, P6.

ARTICLE III: ATTRIBUTING ATTENTION: THE USE OF HUMAN-GIVEN CUES BY DOMESTIC HORSES (*EQUUS CABALLUS*)

(Proops, L. & McComb, K. 2009. *Animal Cognition*, 13, 197-205)

Abstract

Recent research has shown that domestic dogs are particularly good at determining the focus of human attention, often outperforming chimpanzees and hand-reared wolves. It has been suggested that the close evolutionary relationship between humans and dogs has led to the development of this ability; however, very few other domestic species have been studied. We tested the ability of 36 domestic horses to discriminate between an attentive and inattentive person in determining whom to approach for food. The cues provided were body orientation, head orientation or whether the experimenters' eyes were open or closed. A fourth, mixed condition was included where the attentive person stood with their body facing away from the subjects but their head turned towards the subject while the inattentive person stood with their

body facing the subject but their head turned away. Horses chose the attentive person significantly more often using the body cue, head cue, and eye cue but not the mixed cue. This result suggests that domestic horses are highly sensitive to human attentional cues, including gaze. The possible role of evolutionary and environmental factors in the development of this ability is discussed.

Introduction

The ability to attribute attention to others would have obvious adaptive advantages, potentially allowing an animal to more efficiently detect the presence of predators and competitors, follow the gaze of others to significant events and locations, and to engage in more effective communication. There is currently much interest in discovering the prevalence of attention attribution skills across taxa, specifically in determining the cues employed by different species and the extent to which animals have an understanding of the mental states underlying attention. For domestic dogs (*Canis lupus familiaris*), humans represent significant social partners and dogs appear to be particularly adept at reading human cues and body language. Research has shown that dogs can use body, head and often eye cues to determine the attentional state of handlers across a variety of tasks such as obeying commands, fetching toys, locating hidden food and deciding whom to approach for food (Brauer et al. 2004; Call et al. 2003; Gácsi et al. 2004; Miklósi et al. 1998; Schwab and Huber 2006; Soproni et al. 2001, 2002; Virányi et al. 2004). Dogs also distinguish between situations in which a person is looking into space compared to when they are looking at something in particular - suggesting that they may have some appreciation of the communicative intent of gaze (Soproni et al. 2001; Virányi et al. 2004).

Perhaps surprisingly, findings from primates have been more mixed. Despite apes appearing to know what others can and cannot see and having a rudimentary understanding of the relationship between seeing and knowing (Bulloch et al. 2008; Hare et al. 2000, 2001), results from begging, gaze

following and object-choice tasks suggest that untrained apes are less sensitive to eye cues than dogs and tend to rely on head and body cues (Kaminski et al. 2004; Povinelli and Eddy 1996; Tomasello et al. 2007). Other studies of attention getting behaviour, gaze following and competitive food tasks suggest that some primates are capable of using eye cues in certain contexts (Ferrari et al. 2000; Flombaum and Santos 2005; Hostetter et al. 2007; Vick and Anderson 2003). Whether these apparently contradictory results are a methodological artefact or represent a genuine lack of sensitivity is currently unclear (Barth et al. 2005; Hare and Tomasello 2004; Hattori et al. 2007). However, what is clear is that dogs do show an ability to generalise and a level of flexibility across a variety of attention attribution tasks that has not to date been seen in other species including primates.

There are a number of possible explanations for this well-developed ability in dogs that are not mutually exclusive. It may be that domestic dogs have inherited this ability from wolves, that dogs learn to read human cues through enculturation, or that during the process of domestication, dogs have evolved such an ability through a process of selection and convergent evolution (Hare et al. 2002). Very few species have been domesticated, which suggests that there is something "special" about those that have, however, research comparing hand-reared wolf and dogs puppies have produced mixed results. Some studies have found wolves (*Canis lupus*) to be less able to use human cues than dogs, less able to use eye contact and to solicit joint attention (Hare et al. 2002; Miklósi et al. 2003; Virányi et al. 2008) suggesting that the dogs have not inherited their human-reading abilities from their ancestors. Conversely, one recent study found wolves to be more skilled at using human cues than dogs and attributed the poor performance of wolves in previous studies to the test environment (Udell et al. 2008). While intense enculturation and training appears to improve the ability of some species to read human cues including apes (Itakura et al. 1999; Povinelli and Eddy 1996), dolphins (Pack and Herman 2004; Tschudin et al. 2001), seals (Scheumann and Call 2004; Shapiro et al. 2003), ravens (Schloegl et al. 2008) and parrots (Giret et al. 2008), in dogs this skill is present very early in development and does not appear to improve significantly with age (Agnetta et al. 2000; Gácsi et al. 2008; Riedel et al. 2008).

Studies of other domesticated species indicate that the adaptive changes undergone by dogs during domestication may not have made them uniquely skilled at reading human behaviour. Cats can also use human pointing cues in an object-choice task and goats, believed to have been the second species to be domesticated but not having such a close relationship with man as dogs, are able to use pointing and tapping cues, but could not use head direction and gaze alone (Kaminski et al. 2005; Miklósi et al. 2005). The goats tested in the study by Kaminski et al (2005) were kept in a zoo and had little human contact and so lacked the intense enculturation that domestic dogs undergo. As with dogs, this ability to use human pointing gestures did not improve with age and did not improve during the trials, also suggesting that this ability was not learnt during the test or over the subject's lifetime.

In our study, we set out to test the ability to read human cues to attention in another domestic species, the horse. Horses were the last of the five main livestock mammals (goats, sheep, cattle, pigs and horses) to be domesticated around 3500 BCE and as such may be the species that has undergone the least manipulation during domestication (Clutton-Brock 1999; Outram et al. 2009). The relationship between human and horse represents an intermediate level between dogs that live in human homes, often separated from conspecifics, and farm animals, bred for production, that do not usually have such a close relationship with humans. As a species, horses primarily communicate visually, with body language and very small movements of the head, ears and eyes used as communicative signals (Waring 2003), although vocal signals also play an important role in social communication (Proops et al. 2009). Wild equids are also used to living in heterospecific groups and make use of the signals of other species to detect predators (Goodwin 2002). Each of these factors: the possible pre-existing propensity to use fine head cues, the use of signals from other species, domestication involving a close relationship to man and intense enculturation during their lifetime may well have (to varying degrees), led horses to develop an enhanced ability to read human cues to attention.

However, despite the famous case of Clever Hans demonstrating the extent to which horses are capable of detecting very subtle human gestural cues, surprisingly little research has been conducted into this ability in horses (Pfungst 1965). One pilot study using four horses showed that two were capable of using tapping and one of using pointing gestures to locate hidden food (McKinley and Sambrook 2000) and more recent research has confirmed that horses are able to use a variety of pointing gestures in this situation (Maros et al. 2008). Our study aims to provide a direct examination of the ability of horses to attribute attention to humans by assessing whether they are capable of using body, head and eye cues to attention in a begging task. We used this standard paradigm because it represents a naturalistic situation that does not require extensive training to perform and we tested subjects on single trials for each cue to prevent any learning during the study.

Materials and methods

Study animals

A total of 52 horses began the preliminary tests for the experiment and of these, 36 subjects were included in the final analysis. Twelve subjects were from Woodingdean livery yard, Brighton, UK and 24 from the Sussex Horse Rescue Trust, Uckfield, UK. Ages ranged from 10 months to 38 years (mean 13.70 ± 1.61), and included 19 gelded males and 17 females. At both sites subjects live outside all year round. The horses from Woodingdean yard are privately owned and are brought in from the herd regularly for feeding; some of them are ridden. The horses at the Sussex Horse Rescue Trust are checked once a day but remain with the herd most of the time. As such, the privately owned horses had more exposure to humans at the time of the study, although the extent of prior human enculturation was unknown for many of the subjects. Subjects had no known eyesight problems and were comfortable with being handled.

Procedure

R = release point   E = experimenter position
P = pause point   ▽ = camera point
C = centre point

- - -▷ = test trial routes
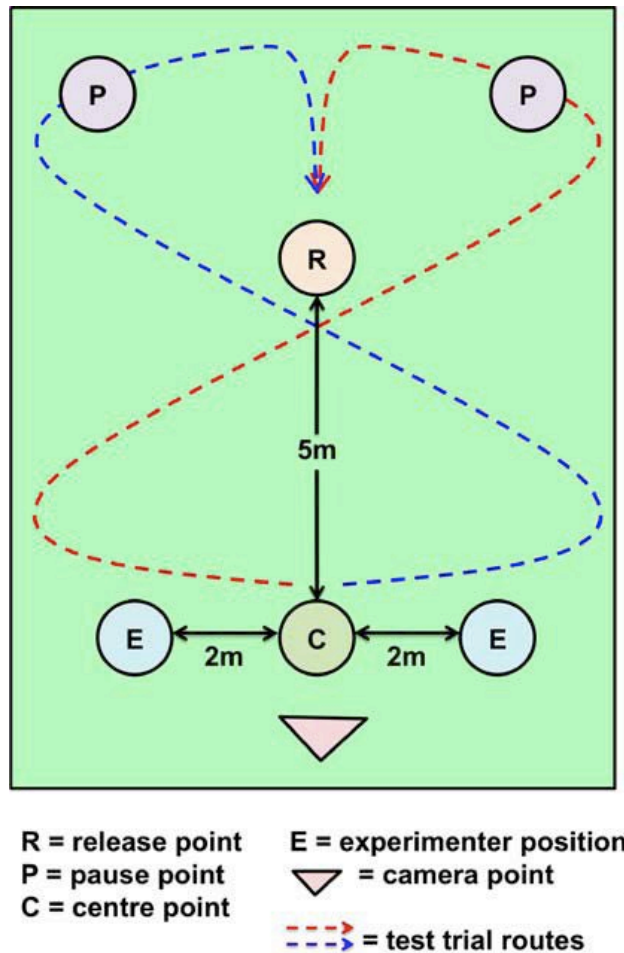
Fig. 1 Diagram of the experimental set-up and test trial procedure.

The test area and test trial procedure can be seen in Fig. 1.

Warm-up phase with attentive experimenters. Twenty-four subjects were given an introductory warm-up phase in which experimenters were facing forwards when giving a reward. This phase began with the subject being held at the release point while the experimenters (A and B) approached the horse from the centre point with their hands outstretched and gave the subject a food reward (commercial horse treats). The experimenters then withdrew to the centre line at point C and the handler (an experimenter familiar to the horses) led the horse to point C to receive another food reward from both experimenters. To prevent the horses developing a preference for one of the experimenters, the reward was administered jointly by crossing over their arms and holding out their hands together with a treat in the middle of both of their hands. The experimenters

also swapped sides between each trial. The response of the horse was gradually shaped so that within a maximum of 10 warm-up trials, the horses were released at point R and would approach the experimenters at point C to receive a reward. Of the 32 subjects that began the test, 4 failed to complete the warm-up phase.

Warm-up phase with inattentive experimenters. Additional trials were run with 12 subjects. Here subjects were presented with a warm-up phase in which the experimenters were not attentive to the subjects and adopted body postures that were not repeated in the test trials. In this phase, the experimenters stood at 90° from the subject facing each other with their hands outstretched together and a reward held in their hands. The horse was lead to the experimenters. Again the response of the horse was gradually shaped so that within a maximum of 10 warm-up trials the horses were released at point R and would approach the experimenters at point C to receive a reward. In these trials, there was no possibility that the horses could be conditioned to cues during the warm-up phase that were later presented in the test trials. Of the 20 subjects that began the test, 6 failed to complete the warm-up phase.

Test trials. The test phase was the same for all 36 subjects. Four cued trials were given to each subject in a counterbalanced order with a reinforcement trial between each test trial. After the warm-up phase, experimenters A and B took up their positions at the points marked E in Fig. 1. For each trial, one experimenter was inattentive and the other was attentive. The side of the attentive person, the identity of the attentive person and the side the experimenters stood on was counterbalanced across trials. No reward was given during test trials. After each test trial, there was a reinforced trial to maintain the motivation of the subjects. In these trials, experimenters A and B returned to point C and adopted the position the subjects had been presented with in the warm-up phase. Subjects were released at point R to approach the experimenters and receive a treat. Subjects were then lead in a figure of eight around the test area, either to the left or the right and then held at point P for 30 s facing away from the centre point before beginning the next trial (Fig. 1). Pilot trials showed that these measures considerably reduced perseveration rates. If

horses failed to respond to a cue, another reinforcement trial was given and the test trial then repeated. Test trials were repeated a maximum of three times before moving on to the next cue and recording a "no response" score for that cue type.

Four cues to attention were tested. Both experimenters adopted neutral facial expressions throughout the trials. The attentive person stood facing forwards and maintained eye contact with the subject as they approached, keeping their head motionless. The inattentive person either stood with their body turned 180° away from the subject (body orientation condition), stood with their body forwards but their head turned away (head orientation condition) or stood with their body and head forwards but with their eyes closed (eyes closed condition). A fourth, mixed condition was included where the attentive person stood with their body turned away from the subjects but their head turned towards the subject while the inattentive person stood with their body forwards but their head turned away (Fig. 2). A male and female experimenter took part in the trials where an attentive posture was adopted during the warm-up phase and two other male experimenters took part in the trials where an inattentive posture was adopted during the warm-up phase; the handler was the same for all trials.

Psychophysical and anatomical estimates of visual acuity in the horizontal streak of the horse retina where ganglion density is highest have provided acuity estimates that range from 16.5 cycles per degree (CPD) to 30.8 CPD (Harman et al. 1999; Timney and Keil 1992). If we take the estimate of visual acuity to be around 23 CPD, this means horses' acuity is about 20/33 compared to humans, so detail a human can see at 8.3 m, a horse can see at 5 m, suggesting that subjects would be able to detect the difference between open and closed eyes at 5 m. This would be consistent with their use of fine head and body movements as a method of communication between conspecifics.
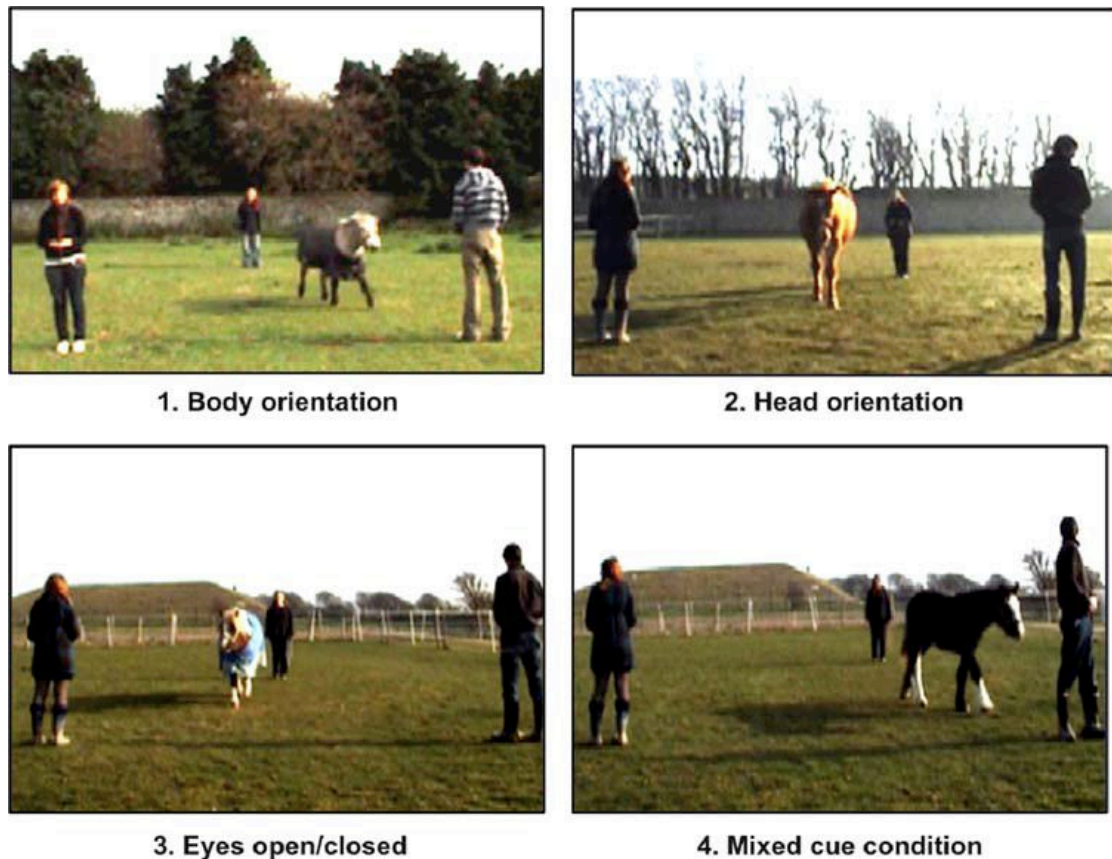
Fig. 2 Still images of the four experimental conditions.

Of the 42 subjects that progressed to the test trials, 6 showed a side bias by choosing the left or right side for all trials (4 subjects exposed to the attentive warm-up phase and 2 exposed to the inattentive warm-up phase) and so their results were excluded from the analysis. Of the 36 subjects that were included in the analysis, 2 subjects failed to choose an experimenter for three consecutive mixed cue trials and so were given a "no response" score for that cue type.

Behavioural and statistical analysis

Trials were recorded using a Sony digital handycam DCRTRV19E video recorder and were converted to .mov files and analysed frame by frame (frame = 0.04 s) on a Mac G4 powerbook using Gamebreaker 5.1 video analysis software [31]. The main behaviour studied was whether the subjects correctly chose the attentive person over the inattentive person when determining whom

to approach to receive food. A choice was defined as correct if the subject approached and stood within 1 m of the attentive experimenter within 60 s of being released. The number of subjects correctly choosing the attentive person for each trial type was analysed using binomial tests. Fisher's exact tests were used to compare the accuracy of responses to each cue for subjects given the two different warm-up phases. Overall side and experimenter preferences were assessed using binomial tests. The total number of correct scores was calculated for each subject and effects of sex and age were analysed using a Mann–Whitney U test and a Spearman's ρ correlation, respectively. We also predicted that there might have been a difference between the subjects from the livery yard that had regular interactions with humans and the animals at the horse sanctuary who currently had less exposure to humans on a day-to-day basis, and may have had more negative experiences with humans prior to arriving at the sanctuary. This possible effect was also analysed using a Mann–Whitney U test.

In addition to assessing whether subjects were able to make the correct choice of whom to approach for food, we also recorded the time it took for horses to make a response. Response times were defined as the time between the release of the subject and the time at which the horse stopped moving and was within 1 m of either of the experimenters. Reaction time data were positively skewed and so were $\log_{10}$ transformed. The effects of trial type and response accuracy (correct/incorrect) were analysed as fixed factors in a linear mixed model with a scaled identity covariance structure. The model was run using a maximum likelihood estimation.

Results

The number of correct responses given to each cue by the subjects exposed to attentive experimenters compared to the inattentive experimenters in the warm-up phase was not statistically different (Table 1). This demonstrates that the horses' responses during the test trials were not conditioned by specific cues

that were given during the warm-up phase. Results from the two groups were therefore pooled for further analysis.

Table 1 Comparison of accuracy rates for subjects given the warm-up trials in which experimenters were attentive compared to inattentive.

Cue	Attentive warm up		Inattentive warm up		FET (P)
Body	19/24	79%	9/12	75%	$p > 0.99$
Head	17/24	71%	8/12	67%	$p > 0.99$
Eyes	19/24	79%	9/12	75%	$p > 0.99$
Mixed	13/22	59%	5/12	42%	$p = 0.48$

Results of Fisher's Exact Tests (FET) comparing the difference between the two results are shown.

Main effect

Results show that the horses chose the attentive person significantly more often than the inattentive person using the body cue ($n = 36$, $K = 28$, $P = 0.001$), the head cue ($n = 36$, $K = 25$, $P = 0.029$) and the eye cue ($n = 36$, $K = 28$, $P = 0.001$) but not the mixed cue ($n = 34$, $K = 18$, $P = 0.864$) (Fig. 3).

Total scores were not correlated with age ($r_s = -0.048$, $P = 0.780$). Overall, females performed significantly better than males ($n_1 = 17$, $n_2 = 19$, $U = 93.0$, $P = 0.016$) although both groups had a median score of 3. There was no difference between overall scores for subjects from the two locations ($n_1 = 24$, $n_2 = 12$, $U = 103.0$, $P = 0.129$). In addition, there were no overall side ($n = 142$, $K = 76$, $P = 0.450$) or experimenter biases across subjects (trials with attentive experimenters during warm-up phase $n = 94$, $K = 51$, $P = 0.470$; trials with inattentive experimenters during warm-up phase $n = 48$, $K = 28$, $P = 0.312$).
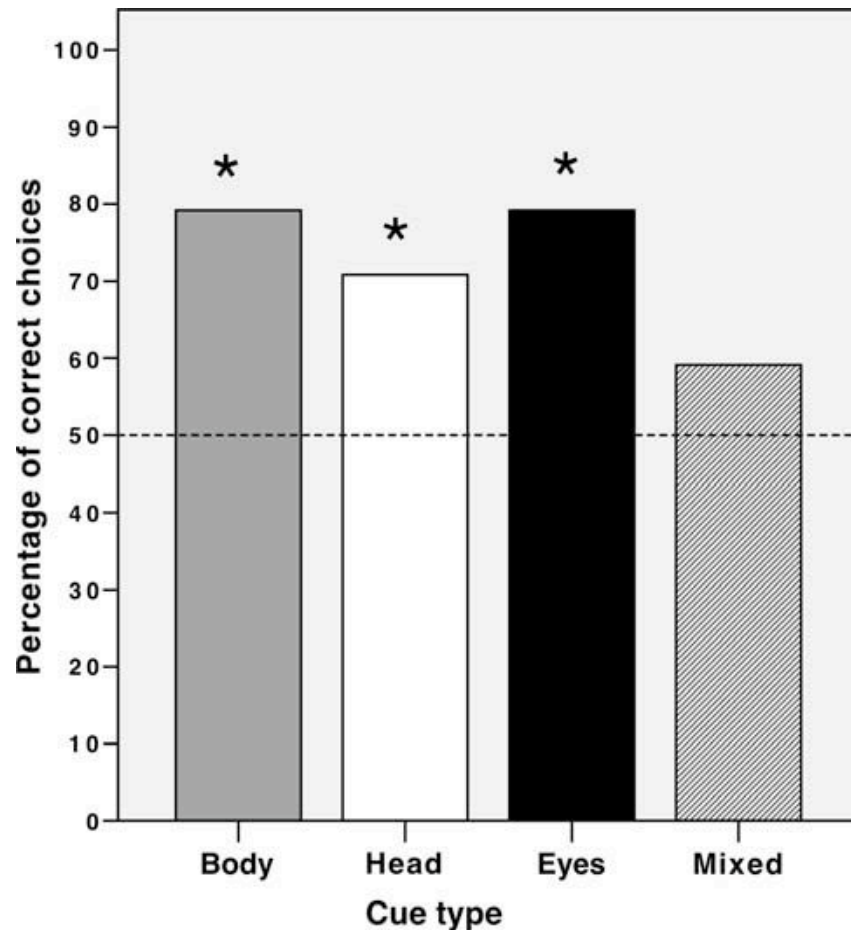
Fig. 3 Percentage of horses correctly choosing the attentive person for each cue type. * = $P < 0.05$ (binomial probabilities, two-tailed predictions).

Response times

Overall response times were longer for incorrect compared to correct trials ($F_{1, 141} = 7.403$, $P = 0.007$) although there was no significant main effect of cue type on response times ($F_{3, 141} = 1.356$, $P = 0.259$). The interaction effect of cue type and accuracy on response times was significant ($F_{3, 141} = 3.951$, $P = 0.010$). More specifically, response times tended to be slower when horses were making the wrong choice on the basis of body and head cues but not when choosing on the basis of eye and mixed cues (Fig. 4).
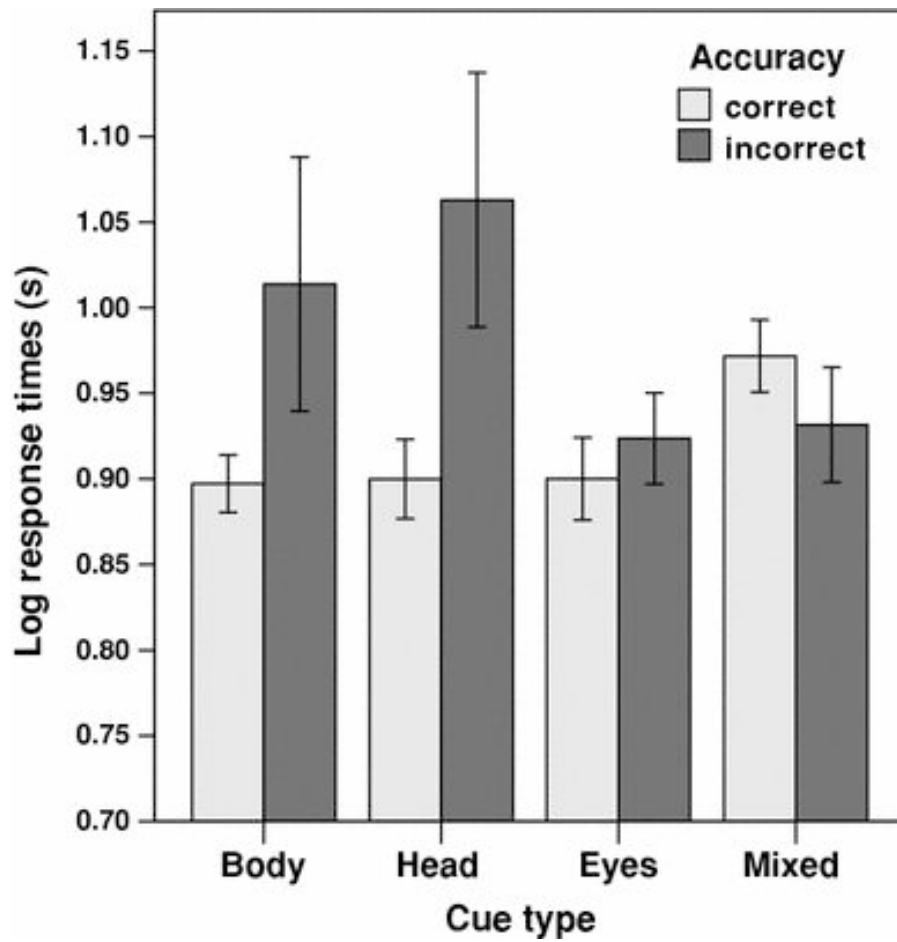
Fig. 4 Mean response times for correct and incorrect choices for each cue type.

Discussion

These results show that horses are highly skilled at reading human cues to attention and are capable of using subtle eye cues (possibly by detecting fine movement of the eyes) as well as "grosser" cues such as body and head orientation to select the more attentive of two people. The level of accuracy was similar across the body, head and eye cue trials, suggesting subjects were equally able to utilise each cue. However, reaction times reveal that subjects took longer to reach a decision when making an incorrect choice (approaching the inattentive person) on the basis of head and body cues, indicating that they were less sure of their decision on these occasions. Conversely, when using the finer scale eye cue there was no difference in decision times for correct and incorrect choices so subjects did not appear to have an underlying awareness

of whether they were making the wrong choice. Thus horses may process these cues in different ways.

The differences in reaction times for incorrect compared to correct choices for the body and head cues also indicate that the horses may have been discriminating between attentive and inattentive experimenters to a higher degree than is apparent in their choice of person alone. In a similar way, although dogs do not show a strong preference towards fetching a toy to owners when their eyes are visible compared to when their eyes are obscured with a blindfold, they do approach more hesitantly (Gácsi et al. 2004). Primate studies have also pointed to a discrepancy between the accuracy of the overt response to cues and more unconscious measures of responding such as looking time (Hattori et al. 2007). In our study, subtle behaviour (hesitancy) revealed greater discrimination between cues than more overt responding.

It is also worth noting that four of the eight subjects which approached the inattentive person given the body cue moved round to the front of the person possibly to enter the experimenter's field of vision. Horses also used tactile gestures such as nudging the experimenters when they were not rewarded. This suggests that even when they chose the inattentive person they may have been using strategies to gain their attention. Recent research confirms that horses, like primates, can adjust the mode of their communication based on the attentiveness of their handler (Hostetter et al. 2001; Leavens et al. 2004; Takimoto and Fujita 2008).

Subjects did not preferentially choose the experimenter facing them during the mixed cue trials. There are two ways to interpret this finding: either they do not have a hierarchical interpretation of attention cues and fail to appreciate that eye (and head) cues are more salient than body cues, or they may interpret the turned body as a signal that the experimenter does not intend to cooperate with them. This second interpretation was put forward as a possible explanation of similar findings in apes (Kaminski et al. 2004). In this way, failure to approach the person facing forwards but with their body turned away, may not represent a failure to attribute attention but instead, an active attribution that the turned back

signals a lack of intention or ability to provide food. This current study cannot distinguish between these two possible explanations and, indeed there is still debate as to whether humans process body, face and eye cues hierarchically or in parallel (Gácsi et al. 2004).

Another interesting result was that females were more likely to choose the attentive experimenter than males. In free-ranging horse societies, older mares are often instrumental in maintaining social cohesion within the group and determining their daily movement; long-lasting bonds between female horses are commonplace and in this sense horse societies have been described as matriarchal (Goodwin 1999; Jensen 2002; Wells and Goldschmidt-Rothschild 1979). This result would suggest that females may possess enhanced social discriminative abilities as has been reported in other matriarchal societies (McComb et al. 2000, 2001). However, recent research has not shown domestic female horses to be more skilled than males at recognising close associates (Proops et al. 2009), neither has this sex difference been reported in previous studies of human attention attribution conducted with other species. Further research with a larger sample size would be required to investigate these preliminary findings.

Overall, subjects were able to use body, head and eye cues in our begging task, indicating that horses may well be as skilled as dogs and more skilled than all but the most intensely enculturated apes at this specific task. In this study horses were presented with one trial per cue, therefore, subjects did not have the opportunity to learn to discriminate cues during the task. This factor combined with the finding that horses were as accurate at attributing attention given a warm-up phase with inattentive compared to attentive experimenters, suggests our experiment provides a test of their pre-existing knowledge about human attentional states. Taken together with other findings indicating that horses are able to use complex human cues in object-choice tasks, these results point towards an enhanced ability to read human cues in domestic horses. In the same way that there are three explanations for enhanced abilities to read human communicative cues in dogs, there are also three main explanations for this skill in horses. Domestic horses may have learnt these

abilities through intense enculturation throughout their lifetimes or, through the process of domestication, evolved a particular sensitivity to human communicative cues, or inherited a general skill for the discrimination of social cues from their wild ancestors.

The absence of a correlation between age and ability in our experiments and the accurate performance of a 10-month-old foal (and other youngsters) in the study suggests that the social sensitivity observed may have a strong genetic component and/or is learnt very early in development. Further research specifically looking at the ontogeny of this ability in foals (akin to previous studies of puppies) would help to elucidate more clearly the role of genes and environment in its development. Similarly, comparisons between adult subjects with different training/human exposure histories would also be of benefit. "Natural horsemanship" training techniques, typified by trying to take into account natural horse behaviour during training and also with a strong emphasis on ground work, appears to produce adult horses better able to use human cues such a pointing in an object-choice task (Bartosova et al. 2008; McKinley and Sambrook 2000). Whether training plays a role in development of attention attribution skills is unclear. We found no difference between subjects based on their current level of human interaction, however, as is often the case with studies of adult horses, it was not possible to obtain full life histories for many of the subjects and so the effects of prior experience on their abilities could not be adequately assessed (Cooper 2007). It also remains to be seen whether domesticated horses perform better than their wild cousins or other equid species, when socialised to comparable levels. So far, this analysis of pre-existing phylogenetic skills via direct comparison between domesticated and wild species has only been conducted with dogs, wolves and domesticated Silver foxes.

By studying the ability of horses to attribute attention to people across a variety of tasks, we can determine the extent to which horses are able to use eye and body cues flexibly. Traditional animal management techniques often state that direct eye contact is seen by many species, including horses, as an aggressive act, although there has been very little empirical evidence to confirm this (Vervill

and McDonnell 2008). In the same way that humans distinguish between a stare of aggression and a look of friendship, this current research suggests that horses will interpret eye contact as a friendly gesture in certain contexts. Future research investigating the cues and contexts in which horses interpret gaze as a positive or negative cue will help to determine the sensitivity and flexibility with which horses interpret human gaze. This may also help to clarify whether recognition of attentional states occurs as a strictly behavioural, discrimination learning process or whether the ability operates at a more cognitive, rule-based level.

In order to understand the evolution of social intelligence, the development of attention attribution skills and how they relate to other abilities such as theory of mind, it is necessary to test a wide variety of domestic and wild animals across a range of tasks. It is clear from our results that horses are highly sensitive to human gestural cues including gaze. Although the factors which give rise to this ability are likely to vary across taxa, the high numbers of correct responses on first trials, the lack of correlation between age and performance, and the accurate performance of some very young subjects in this study suggest that horses, like dogs, may have a pre-disposition to be highly sensitive to human attentional cues.

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ARTICLE IV: THE USE OF HUMAN-GIVEN CUES BY DOMESTIC HORSES, *EQUUS CABALLUS*, DURING AN OBJECT CHOICE TASK

(Proops, L., Walton, M. & McComb, K. 2010.
Animal Behaviour*, 79, 1205-1209)*

Abstract

Selection pressures during domestication are thought to lead to an enhanced ability to use human-given cues. Horses fulfil a wide variety of roles for humans and have been domesticated for at least 5000 years but their ability to read human cues has not been widely studied. We tested the ability of 28 horses to attend to human-given cues in an object choice task. We included five different cues: distal sustained pointing, momentary tapping, marker placement, body orientation and gaze (head) alternation. Horses were able to use the pointing and marker placement cues spontaneously but not the tapping, body orientation and gaze alternation cues. The overall pattern of responding suggests that horses may use cues that provide stimulus enhancement at the time of choice and do not have an understanding of the communicative nature of the cues given. As such, their proficiency at this task appears to be inferior to that of domestic dogs, *Canis lupus familiaris*, but similar to that of domestic goats, *Caprus hircus*.

Introduction

The ability to acquire information about the external world from the communicative gestures of social partners has obvious adaptive advantages and raises intriguing questions about the sensitivity of receivers to the underlying mental states of signallers. The extent to which animals use human cues to locate hidden food has been effectively studied using the object choice task. In this paradigm subjects are presented with two or three opaque

containers and human experimenters provide gestural cues as to the location of hidden food. A wide variety of species have been studied using this protocol, primarily domestic dogs, (e.g. Miklósi et al. 1998) and nonhuman primates (e.g. Povinelli et al. 1997; Byrnit 2009) but also other species including wolves, *Canis lupus* (e.g. Hare et al. 2002), domestic cats, *Felis catus* (Miklósi et al. 2005), domestic goats (e.g. Kaminski et al. 2005), South African fur seals, *Arctocephalus pusillus* (e.g. Scheumann & Call 2004), bottlenosed dolphins, *Tursiops truncatus* (e.g. Pack & Herman 2004), jackdaws, *Corvus monedula* (e.g. von Bayern & Emery 2009), ravens, *Corvus corax* (e.g. Schloegl et al. 2008) and domestic horses (Maros et al. 2008).

It has been suggested that domestication has led to an enhanced ability to read human cues and domestic dogs show a flexibility and ability to generalize in the object choice task that has not been seen in other species (Miklósi et al. 1998; Hare et al. 2002, 2005). Their ability to use a wide variety of cues from the first trial (Miklósi et al. 1998; Agnetta et al. 2000; Miklósi & Soproni 2006) and the fact that they distinguish between situations in which a person is looking at a target object and ones in which they are looking above the target object suggest that they may have some appreciation of the referential nature of these cues (Soproni et al. 2001). Cats have also been found to use a variety of pointing cues including momentary distal pointing (Miklósi et al. 2005). However, other domestic animals have not performed as well. Goats spontaneously use pointing and tapping cues but not head and gaze orientation alone, indicating that they may be using the more basic mechanism of stimulus enhancement rather than comprehending the communicative nature of the cues provided (Kaminski et al. 2005).

The results from primate studies have been much more mixed and are difficult to interpret. Many primates perform poorly in object choice tasks and appear to have to learn the cues as discriminative stimuli through the testing process (Povinelli et al. 1997, 1999; Tomasello et al. 1997; Hare & Tomasello 2005; Byrnit 2009). However, other studies using highly enculturated subjects, or slightly different methodologies including competitive rather than cooperative paradigms, have shown that some primate subjects are able to use pointing

and more subtle human cues such as gaze (Itakura et al. 1999; Hare & Tomasello 2004; Barth et al. 2005; Mulcahy & Call 2009). This suggests the poor performance of some primate subjects may be caused by motivational rather than cognitive factors. Indeed, in one object choice study, apes that were trained to use a marker placed by an experimenter used this cue only if it appeared the experimenter placed the marker intentionally rather than by accident (Call & Tomasello 1998). This result suggests that some primates are sensitive to the intent underlying human action.

To understand the proximate and ultimate factors that produce an ability to use human-given cues, it is important to test a wide variety of domestic and wild species. Horses have been domesticated for at least 5,000 years (Clutton-Brock 1999; Outram et al. 2009) and to date two studies have conducted object choice tests with domestic horses. However, limited sample sizes and types of cue tested do not allow any firm conclusions to be drawn about the processes underlying the behaviours observed. The first study required the operant conditioning of horses to retrieve food from an upturned bucket, making the task much harder than simply approaching a particular container (McKinley & Sambrook 2000). Here only four of the 11 subjects that were recruited completed the training phase and, of those, one subject could use a dynamic pointing cue and two could use a dynamic-sustained touching cue. In the second, more extensive study, horses were simply required to approach one of two buckets to look for food. In this study 20 of 27 horses completed the training phase and results indicated that subjects could use pointing cues when the finger was close to the target and distal pointing if it was sustained but not when the hand was removed before the choice was made (Maros et al. 2008). Thus the horses appeared to perform much better in the second study, possibly because the more complicated methodology in the other study hindered the performance of subjects. Further work is therefore required to determine why these differences are observed and to test horses with new types of cue.

Our new experimental paradigm tested existing object choice skills by using a simple method of requiring subjects to approach one of two buckets rather than training subjects to overturn buckets themselves to find food. Moreover, we

tested for abilities to use a more extensive range of cues to throw light on the proximate mechanisms used in this task and to allow for greater comparison of cue use between species. Previous observations of horses performing the object choice task reveal that, when using the pointing cue, subjects tend to approach the experimenter's hand before choosing the nearby bucket (McKinley & Sambrook 2000; Maros et al. 2008). This suggests that horses, like goats, may be using stimulus enhancement to choose the correct container. To determine whether this is the process used, we included cues that did not involve stimulus enhancement: body orientation and gaze alternation and also a momentary tapping cue that only provided stimulus enhancement temporarily, prior to the time when the choice was actually made. We also assessed the ability of horses to use a totally novel cue, the placement of a marker in front of the correct bucket, and included a distal sustained pointing cue to help interpretation of previous studies.

Methods

Subjects

A total of 34 domestic horses from four locations participated in this study. Of these subjects, 28 (11 females and 17 gelded males) completed the initial warm-up phase and took part in the test trials. Ages ranged from 3.5-38 years (X+SE = 13.16+1.54). Subjects were privately owned, riding school horses or were rescue animals kept at a horse sanctuary. Horses kept at private yards or the riding school had daily interaction with humans; the horses at the sanctuary were checked once a day but remained with the herd most of the time. Subjects were not food deprived prior to the study. The study was approved by the University of Sussex Ethics board.

Procedure

Trials were conducted January-March 2009 in a paddock or school depending on the location of the subjects. The set-up procedure can be seen in Fig. 1.

R = release point   E = experimenter position
P = pause point   B = bucket position
▽ = camera point   b = bucket position in
= test trial routes   warm-up phase
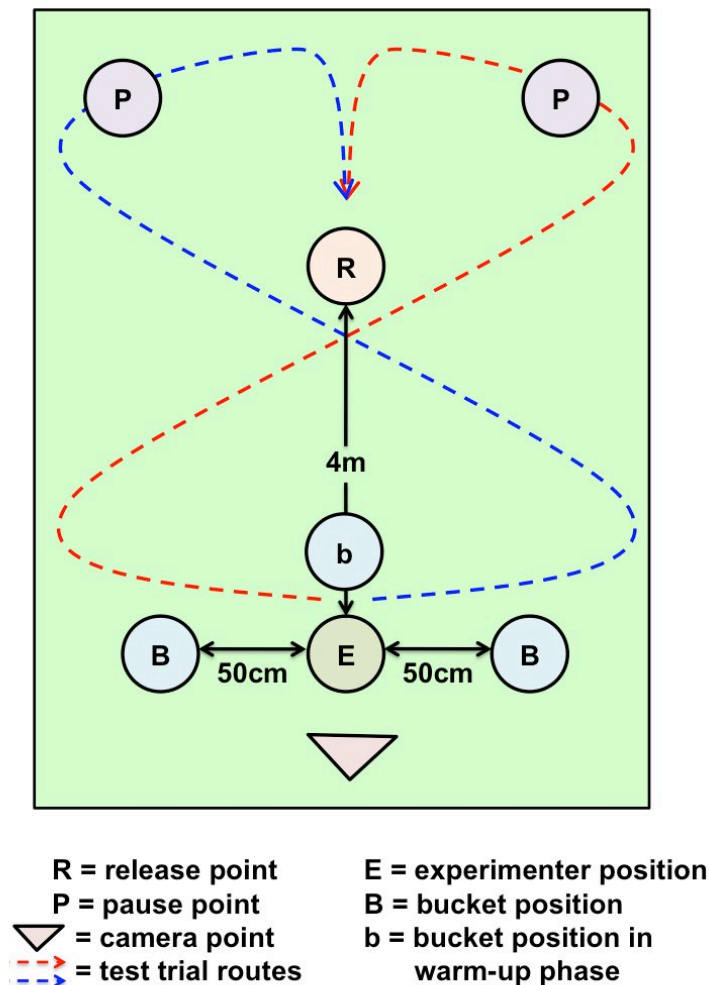
Fig. 1. Diagram of the experimental set-up and test trial procedure.

The experimenter providing the cues was a female unknown to the subjects and the handler was a female experimenter that the subjects had not or only rarely encountered before. Subjects were led from the left side at all times. An initial reinforcement phase was given to each subject to create an association between the experimenter, buckets and a food reward. The experimenter stood at centre point E with two black buckets (40 cm diameter, 19 cm height) stacked together in front of her. As the subject was led along the centre line towards point E, the experimenter dropped a piece of carrot into the bucket for the subject to collect. The horse was then led in a semicircle to the left or the right, returned to the centre line and the reinforcement trial repeated. Over a maximum of 10 trials the behaviour of the horse was gradually shaped so that it

could be released at a point on the centre line 4 m from the experimenter and would walk forwards to take the carrot from the bucket.

Test trials were conducted immediately after the reinforcement phase. In these trials, two buckets were placed 50 cm to the left and right of the experimenter. As the horse approached the release point, the experimenter gave one of five cues towards one of the buckets. The horse was then released to move forwards towards the buckets while the handler remained at the release point until the trial was completed. If the horse chose the bucket that was cued, a reward was placed in the bucket by the experimenter as soon as the decision had been made. The carrot was not placed in the bucket before the choice was made to prevent any odour cues and to ensure that the horses could not see the carrot in the bucket as they approached the containers. The side of the cue was counterbalanced across subjects with half receiving three cues to the left and half receiving three to the right. The order was pseudorandomized with the constraint that trials in which a response was given could not cue the same side more than twice in a row. The order of cue presentation was counterbalanced across trials with each cue being presented first, second, third, fourth and fifth an equal number of times. After each test trial there was an additional reinforcement trial to maintain the motivation of the subjects. In these trials the buckets were again placed in front of the experimenter and a piece of carrot placed in the bucket as the horse approached. Subjects were then led in a figure of eight around the test area, either to the left or the right and held, facing away from the centre at point P for 30 s before beginning the next trial (see Fig. 1). Pilot trials showed that pausing between test trials, leading horses in a figure of eight so they travelled across both the left and right side of the test area before each trial and introducing a reinforcement trial between each test trial considerably reduced perseveration rates and improved response rates. If horses failed to respond to a cue, another reinforcement trial was given and the test trial then repeated. Test trials were repeated a maximum of three times before moving on to the next cue and recording a 'no response' score for that cue type. One horse failed to respond to the body cue.

We tested the following five cues.

(1) Marker placement cue: a blue and yellow striped wooden block (18.5 × 7 × 3.5 cm) was used as the marker. As the horse approached the release point the experimenter placed this on the ground in front of, and touching, the correct bucket. She then returned to a standing posture, body oriented forwards, looking directly ahead.

(2) Distal sustained pointing cue: as the horse approached the release point the experimenter brought her ipsilateral arm out from the side of her body to point towards one of the buckets. This position was held with the body oriented forwards, looking directly ahead until a choice was made. The index finger was approximately 65 cm from the top of the bucket.

(3) Momentary tapping cue: as the horse approached the release point the experimenter reached towards the correct bucket and tapped the side of the bucket slowly three times with large movements of the arm producing an audible sound each time. She then returned to a standing posture, body oriented forwards, looking directly ahead.

(4) Body orientation cue: as the horse approached the release point the experimenter turned her whole body towards the correct bucket and stood looking down at the bucket until a choice was made.

(5) Gaze alternation cue: keeping her body oriented forwards, the experimenter alternated the direction of her head and gaze between the horse and the correct bucket until a choice was made.

Behavioural and statistical analysis

Trials were recorded using a Sony digital handycam TRV 19E video recorder and converted to .mov files for behavioural analysis. A choice was recorded as correct if the subject's head approached within 20 cm of a bucket within 60s of being released. In most trials subjects touched the chosen bucket but in some cases subjects looked into the bucket without touching it. Responses were coded live and verified by two independent experimenters using the video footage. Interobserver reliability was 0.96 ($P < 0.0001$) measured by Spearman ρ correlation. To test for a difference in the number of correct and incorrect responses given to the five different cue types, a Pearson chi-square test was

used. Additional post hoc contrasts were performed on 2 × 2 tables. Where expected values were greater than 5, the chi-square values are reported and in the one case where expected values were less than 5, the Fisher's exact test (FET) is reported. The Bonferroni correction was not used with this small sample because of the high likelihood of Type II errors; instead we report effect sizes in the form of Cramer's *V*, as suggested by Nakagawa (2004). Effect sizes reflecting the strength of the relationship between variables, such as Cramer's *V*, are considered small, medium and large at values 0.1, 0.3 and 0.5, respectively (Nakagawa 2004). The number of subjects correctly choosing the cued bucket for each cue type was analysed using two-tailed binomial tests. The total number of correct scores was calculated for each subject and the effects of age and location were analysed using a Spearman ρ correlation and a Kruskal-Wallis one-way analysis of variance test. Overall side biases were assessed using a Wilcoxon signed-rank test. All statistical analyses were performed using SPSS version 16.0.1 software for Mac (SPSS Inc., Chicago, IL, U.S.A.).

Results

There were significant differences in the horses' ability to use the five cues (χ^2_4 = 13.887, *P* = 0.008, *V* = 0.316). Horses used the marker placement (*N* = 28, *K* = 26, *P* < 0.0001) and pointing cues (*N* = 28, *K* = 23, *P* = 0.001) to choose the correct bucket but not the tapping (*N* = 28, *K* = 16, *P* = 0.572), body orientation (*N* = 27, *K* = 16, *P* = 0.442) or gaze alternation cues (*N* = 28, *K* = 17, *P* = 0.345) (see Fig. 2). Post hoc analyses revealed that there were significant differences between the ability of subjects to use the marker cue compared to the tapping (χ^2_1 = 9.524, *P* = 0.002, *V* = 0.412), gazing (χ^2_1 = 8.114, *P* = 0.004, *V* = 0.381) and body orientation cue (χ^2_1 = 8.586, *P* = 0.003, *V* = 0.395). In these comparisons the effects of the different cues were medium/large. There was no significant difference between the use of the marker and pointing cues (FET: *N* = 56, P = 0.422, *V* = 0.162). The difference between the ability of horses to use the pointing cue compared to the tapping was also significant (χ^2_1 = 4.139, *P* = 0.042, *V* = 0.272), while the comparison between performance of subjects given

the pointing cue compared to the body orientation (χ^2_1 = 3.489, P = 0.062, V = 0.252) and gaze cues approached significance (χ^2_1 = 3.150, P = 0.076, V = 0.237). Here the effect sizes were medium/small. There were no differences in the ability of horses to use the tapping cue compared to the body orientation cue (χ^2_1 = 0.25, P = 0.874, V = 0.021) or the gaze cue (χ^2_1 = 0.074, P = 0.786, V = 0.036) or in their ability to use the body cue compared to the gaze cue (χ^2_1 = 0.012, P = 0.912, V = 0.015).
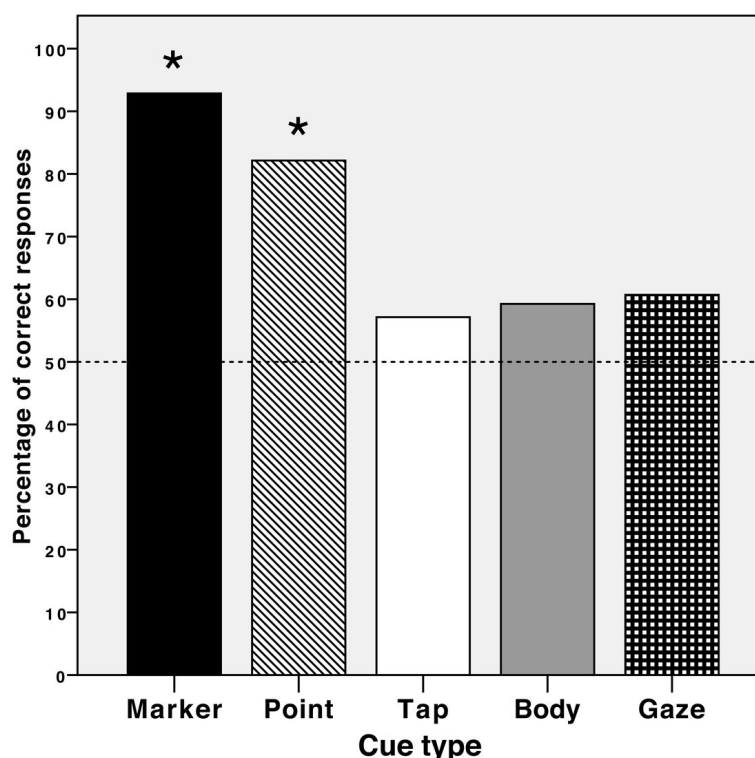
Fig. 2. Percentage of correct responses for each cue type. * = P < 0.05 (binomial probabilities, two-tailed predictions).

Of the 23 subjects that correctly used the pointing cue, 14 investigated the outstretched arm before moving to the bucket. All of the subjects that correctly chose the bucket given the marker placement cue investigated the marker before investigating the bucket.

Total scores across all cue types were not correlated with age (r_s = -0.325, N = 28, P = 0.091). There was no difference in the total scores of the subjects caused by location (H_3 = 2.255, P = 0.521). There were no overall side biases (z

= 0.478, *N* = 28, *P* = 0.632). At an individual level, one horse consistently chose the left-hand bucket and all other subjects chose each side at least once across the five test trials. Only three of the 28 horses failed to respond to a test trial, with a total of 10 'no responses' recorded within these subjects. One subject failed to respond to the tapping cue twice, another subject failed to respond to the tapping cue once, the gaze cue once, the point cue twice and the body cue three times, and a third subject failed to respond to the pointing cue once.

Discussion

Horses were able to use the pointing and marker placement cues spontaneously to choose between objects but did not use the tapping, body orientation or gaze alternation cues. As such the ability of horses in this respect appears inferior to that of domestic dogs (Miklósi & Soproni 2006). Horses have previously been shown to use subtle cues such as gaze and body orientation when determining the focus of human attention (Proops & McComb, in press); however, they were unable to use these cues in the object choice task presented here. As such their performance could be seen as comparable to that of domestic goats, although goats were able to use a continuous dynamic touch cue whereas horses could not use a momentary tapping cue (Kaminski et al. 2005). The ability of horses to use the pointing cue confirms the findings of Maros et al. (2008) that horses are able to use a distal sustained point as a cue to locate food and suggests that the poor performance of horses in the McKinley & Sambrook (2000) study may be because of the more complex methodology used. This conclusion is further confirmed by the high 'drop out' rate in the McKinley & Sambrook (2000) study (64%) compared to that found in our study (18%) and Maros et al.'s (2008) study (26%).

The fact that horses were able to use the pointing and marker placement cues but not the gaze alternation and body orientation cues suggests that horses use stimulus enhancement to choose the correct container, a more basic cognitive mechanism than that used by domestic dogs. This is further confirmed by our observations (and those of previous studies) that when using the pointing cue

many horses initially approached the outstretched hand and only subsequently went to the correct bucket. Similarly, all of the subjects that chose the correct bucket using the marker cue investigated the marker before the bucket, strongly suggesting that it was the marker itself that provided stimulus enhancement and indirectly attracted the horses to the correct bucket. Dogs are able to use markers as cues even when they are removed before a choice is made, but they do not readily use markers if they do not see a human place the marker; thus for dogs, the human element of marker placement appears to be an important factor (Riedel et al. 2006; Udell et al. 2008a). In our study the human element was also involved and so further research with horses incorporating different test permutations would help to clarify the mechanisms involved. If stimulus enhancement alone rather than the human action associated with marker placement was key to the horses' response, then they would be less likely to use the cue if it was removed prior to making the choice (but unlike dogs would still use the cue even if the placement of the marker by the experimenter had not been observed).

Perhaps surprisingly, horses did not appear to use the tapping cue despite this ability being shown in goats and horses previously (McKinley & Sambrook 2000; Kaminski et al. 2005). One difference between our study and previous studies was that in our study the cue was removed before the choice was made, so that at the actual time of choice there was no stimulus enhancement. However, one may have expected that such a salient cue, given only a few seconds before the choice was made, would have been a reliable indicator of the correct bucket. Indeed, Maros et al. (2008) found that horses could use a pointing cue that was removed seconds before the choice was made, providing the cue was given close to the bucket. Another difference between those studies and ours is that in our study an audible sound was made when touching the bucket. Although previous studies have found that the performance of subjects improved when cues were accompanied by audible sounds (Itakura et al. 1999) it is possible that in this case the sound led some subjects to avoid the cued bucket deliberately. Communicative signals can be given in both cooperative and competitive situations and some subjects may have interpreted the audible tapping on the bucket combined with direct gaze of the

experimenter towards the horse as a demonstration of possession of that particular bucket. Primate subjects that did not use a pointing cue to choose a container in a cooperative context used a pointing gesture combined with a firm vocal command ('don't take this one') to avoid a container in a prohibitive context (Hermann & Tomasello 2006). Alternatively, since the food was not placed in the bucket prior to the cue being given, the noise may have signalled to the horses that the bucket was empty. Indeed apes are able to infer the location of hidden food in an object choice task if they hear either the empty or baited container being rattled (Call 2004). To determine why horses did not use this cue, further research could usefully investigate the efficacy of different modes of tapping in cueing object choice, with and without direct eye contact and with and without the bait being placed in the container when the tapping cue is given.

In tests of object choice, the target container is often baited before the subject makes its choice, whereas in our study the reward was placed in the bucket after the choice was made. This design was chosen specifically to avoid the possibility that the horses could choose on the basis of cues emanating from the food itself (colour, odour, etc.) rather than on the basis of the communicative gesture itself (see also Udell et al. 2008b who used a similar method). Rather than signalling the location of hidden food that the experimenter revealed if the correct container was chosen, in our experiment the experimenter presented the gesture in isolation to investigate whether it was spontaneously attended to. Although we believe this is unlikely to change the behaviour of the subjects significantly, the variation in methodology means that we must be cautious in comparing our results to those of other studies. Further research directly comparing the performance of horses given in these different procedures would allow for greater comparison between our findings and those of other studies. As has been noted with these tests of social cognition, relatively small changes in method may lead to significant differences in performance (Barth et al. 2005; Udell et al. 2008b; Mulcahy & Call 2009).

In conclusion, in our study horses demonstrated an ability to use human-given cues in an object choice task that appeared inferior to that seen in dogs but

similar to the ability of domestic goats. Their pattern of responding suggests that, although horses are able to use some cues spontaneously, this may be achieved through a basic cognitive mechanism rather than through understanding the communicative nature of the cues provided. Given that horses have proved inferior to dogs in their ability to read human cues in object choice tasks, it seems unlikely that domestication in general gives rise to highly evolved skills in reading human-given cues; instead it seems more likely that a variety of genetic, ontogenic and environmental factors contribute to this ability.

Acknowledgements

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ARTICLE V: THE RESPONSES OF YOUNG DOMESTIC HORSES (*EQUUS CABALLUS*) TO HUMAN-GIVEN CUES

(Proops, L. & McComb, K. 2011. *PLoS ONE,* in revision)

Abstract

Adult domestic horses are highly sensitive to subtle bodily cues when determining if a person is attending to them but they are less adept at using human cues in an object choice task. Here we provide the first study into the ontogeny of such skills by testing the ability of young horses under the age of 3 to perform these two types of task. In the attention attribution task subjects were presented with an inattentive and attentive person to determine whom to approach for food. Young horses could only use whole body cues to correctly choose the attentive person and could not use more subtle cues such as head movement and open/closed eyes. In the object choice task, subjects were presented with two buckets and a person gave 5 different cues to direct attention to the correct bucket (distal sustained point, elbow point, tapping, body orientation and eye gaze). Young horses, like the adult horses tested previously, were only capable of using the cue that provided clear stimulus enhancement, the distal sustained pointing cue, but not more subtle cues such as gaze and body orientation. These results suggest that the ability of horses to determine whether humans are attending to them using subtle body cues requires significant experience to fully develop. In contrast, their perhaps less remarkable ability to use a cue providing stimulus enhancement in object choice tasks is present at a much earlier age.

Introduction

There is considerable interest in determining the prevalence of attention reading skills across species, not only to gain insights into how these skills

evolved across species but also because it has been suggested that certain attention attribution skills are prerequisites to the development of theory of mind and language in humans. By assessing the phylogeny and ontogeny of these skills we can begin to understand the selection pressures, in combination with environmental factors, which may give rise to abilities to gauge the attentional states of others and discern where their attention is directed. However, to date, research has centred round making comparisons based on the performance of adult individuals of different species and the ontogeny of these skills has not been widely studied outside humans, primates and more recently domestic dogs, *Canis familiaris*.

A large number of species have been assessed for their ability to read human given cues including the great apes [e.g. 1,2], domestic dogs [3, for a review of the literature see 4], wolves, *Canis lupus* [e.g. 5,6], goats, *Caprus hircus* [7], domestic cats, *Felis catus* [8], ravens, *Corvus corax* [9], Clark's nutcrackers, *Nucifraga columbiana* [10], bottlenosed dolphins, *Tursiops truncates* [e.g. 11], South African fur seals, *Artocephalus pusillus* [e.g. 12] and horses [e.g. 13,14]. One task involving reading human cues, that has been given to domestic dogs and domestic horses, involves presenting subjects with two people, one which is attentive to the animal and one which is inattentive (as shown by body, head or eye cues). The subject then has to decide whom to approach to receive food. Another widely used protocol is the object choice task in which subjects are presented with a choice of two or three containers and must approach the correct container to receive a food reward. A person directs their attention towards one of the containers using a particular communicative cue to see if subjects can use this cue to choose the correct container. Cues that have been tested in this task include gazing, tapping, markers and a wide variety of pointing cues including those that are close to the target (proximal points), those that are further away (distal points), those that are present when the choice is made (sustained points) and those that are only given for a short time before the choice is made (momentary points); points have also been given across the body and with different parts of the body including the leg and elbow [3].

There is much debate concerning the mechanisms that may serve to facilitate these human-reading abilities across different species; in particular the extent to which the skills are learnt through exposure to humans during an animals' lifetime and which evolutionary pressures determine levels of performance in different species. It is certainly clear from the performance of non-domestic species such dolphins and seals that learning and enculturation through the individual's lifetime is one route to success in these tasks [11,12]. Similarly, non human primates typically perform surprisingly poorly in studies of human cue use, being insensitive to subtle eye cues when determining attention and being unable to spontaneously use human communicative cues in object choice tasks [1,2,15,16]. However, primates that have been reared in the human environment in a way similar to that of human infants and domestic dogs, perform much better across these tasks suggesting that, through enculturation, they can learn to use these cues [17-19].

However, there is one species in particular that has proved to be highly skilled at reading human cues across a wide variety of tasks, the domestic dog. Dogs are highly sensitive to human body cues including head and eye cues when determining whether a human is paying attention to them [20-24]. Moreover, in object choice tasks they are able to use a wide variety of human given cues including distal sustained pointing and gazing that do not involve any form of local enhancement [25,26]. However, cues that protrude from the human's body and are closer to the container are more salient, with, for example, elbow pointing being less informative than pointing with the whole arm [27]. Dogs are also able to distinguish between instances where humans are looking at an object compared to when they are looking above the object, suggesting they may have some appreciation of the communicative intent behind the cues [28].

These skills in dogs appear to develop at a very early age with puppies as young as 6 weeks old being able to utilise a proximal pointing cues and by 2-4 months of age they are able to use a distal momentary point [29-31]. The early onset of these abilities in puppies and their ability to outperform hand-

reared wolf pups has led to the suggestion that domestication has specifically selected for enhanced human reading skills [5]. However, a recent study of adult hand–reared wolves and shelter dogs suggests that, given sufficient human enculturation wolves are able to utilise distal momentary pointing cues and, conversely, domestic dogs that have not had extensive experience with humans may not [6]. Studies of the ontogeny of these skills in puppies do not necessarily preclude the notion that puppies have learnt at a very early age the relationship between the human caregiver and food. Reanalysis of the data in the Reidel et al [30] study suggests that there may be some learning of the pointing cue during the trials for the 6 week old puppies [32]. It is undeniable that domestic dogs, through an increase in the critical period of socialisation and a reduction in fear and aggression, have gone through adaptation to the human environment [33]. However, rather than also selecting specifically for human-reading skills, it is possible that domestication may have acted indirectly to facilitate this ability in domestic dogs through the acceptance of humans as social partners. This would therefore give them a predisposition to pay attention to and learn human given cues. Such a predisposition may itself be facilitated by an underlying genetic propensity as scroungers to attend to the actions of others [3].

In order to understand more clearly the effects of domestication across species and to assess the proximate mechanisms involved in these tasks, a number of other domestic species have been tested. In the object choice task, domestic goats, with minimal exposure to humans, were able to use a distal sustained point and touch cue [7]. Domestic cats perform at a level comparable to domestic dogs in object choice tasks and are able to use the most challenging point cue – the distal momentary point [8]. Previous studies of adult domestic horses have shown that they are highly sensitive to subtle human cues when determining whom to approach for food (attention attribution task), being able to use head and eye cues as well as gross body cues [13]. Thus in this task they appear to perform as well as domestic dogs. However, in object choice tasks, adult horses do not perform as well as dogs. Horses are able to use the presence of a human, a marker cue and pointing cues if the cue is close to the container or if the cue is sustained during the choice

however, they are not able to use the more difficult distal momentary pointing cue nor gaze or body orientation cues [14,34-36]. This pattern of results coupled with the observation that subjects often approach the outstretched hand or marker before investigating the bucket, has led to the conclusion that horses, like goats, are able to use cues that provide stimulus enhancement but they do not have an understanding of the communicative intent behind the cues. It must be noted however, that horses are able to use a proximal momentary pointing cue and do not use a highly salient momentary tapping cue [for possible explanations of this result see 14], findings which are not totally compatible with the hypothesis that horses only use stimulus enhancement cues.

Here we look for the first time at the human reading skills of young domestic horses. Subjects performed two attention-reading tasks, an attention attribution task and an object choice task. In the attention attribution task, horses were initially exposed to two experimenters that provided food rewards. Following this warm up phase, one experimenter adopted an inattentive posture while the other adopted an attentive posture to determine whom the subjects would then approach to receive a reward. The attentive person stood facing forwards while the inattentive person either stood with their body turned 180° away from the subject (body cue), stood facing forwards with their head turned 90° away (head cue) or stood facing forwards with their eyes closed (eye cue); a forth mixed cue was also given in which the attentive person stood facing forwards with their head directed towards the floor but their eyes looking upwards towards the subject and the inattentive person stood with their body and head facing forwards but their eyes directed towards the floor. To our knowledge, this is the first time such an attention attribution task has been given to young animals. In the object choice task subjects were presented with a choice of two buckets to approach to receive a reward; the experimenter indicated the correct bucket by the use of five cues, a distal sustained point, an elbow point, a momentary tapping cue, orientation of their body in the direction of the correct bucket or alternation of their gaze between the correct bucket and the subject. Subjects were given a single trial for each cue type to prevent any learning during the study. By testing young horses on these tasks we hope

to gain insights into the ontogeny of human reading skills in a previously unstudied species and to see if, like the domestic dog, such skills appear early in development.

Results

Attention attribution task

Young horses chose the attentive person significantly more often than the inattentive person using the body cue ($N = 20$, $K = 17$, $P = 0.003$), but not the head cue ($N = 22$, $K = 11$, $P > 0.99$) the eye cue ($N = 21$, $K = 11$, $P > 0.99$) or the mixed cue ($N = 22$, $K = 10$, $P > 0.83$; see Figure 1).
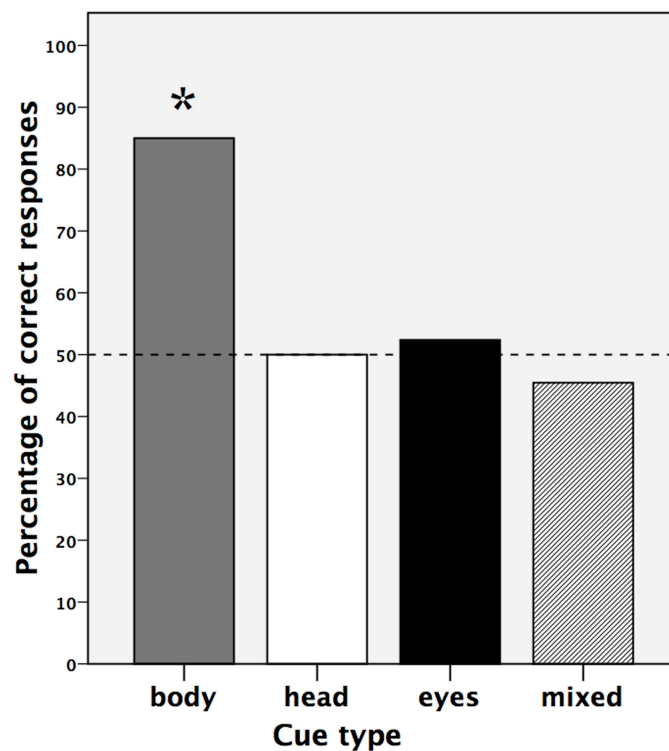
Figure 1. Attention attribution task. Percentage of correct responses for each cue type. * = $p < 0.05$ (binomial probabilities, two-tailed predictions).

There was no significant difference in the total scores of the 3 age groups ($\chi^2_2 = 0.54$, $P = 0.76$) nor was there any significant differences in individual cue use based on age (body cue: $N = 20$, $P = 0.31$; head cue: $N = 22$, $P = 0.75$; eye

cue $N = 21$, $P = 0.64$, mixed cue: $N = 22$, $P = 0.55$). Mean scores were: $X \pm$ S.E. $= 2.25 \pm 0.37$ for subjects under 1yr, 2.40 ± 0.68 for subjects between 1 and 2 and 2.11 ± 0.26 for subjects over 2. In addition, there was no significant difference in the overall performance of subjects according to size ($\chi2_2 = 1.86$, $P = 0.40$) nor was there any significant differences in the number of subjects correctly choosing each individual cue based on size (body cue: $N = 20$, $P > 0.99$; head cue: $N = 22$, $P > 0.99$; eye cue $N = 21$, $P = 0.48$, mixed cue: $N = 22$, $P > 0.99$). Mean scores were: $X \pm$ S.E. $= 2.17 \pm 0.31$ for subjects under 115cm, 2.57 ± 0.37 for subjects between 115cm and 130cm and 2.33 ± 0.56 for subjects over 130cm. There was no significant difference between the performance of males and females ($N_1 = 12$, $N_2 = 10$, $U = 48.0$, $P = 0.41$). Overall subjects chose the person on their right side more often than the person on their left side ($N = 85$, $K = 53$, $P = 0.029$). At an individual level, four subjects showed a right side bias and one showed a left side bias.

Object choice task

Subjects were able to use the pointing cue ($N = 25$, $K = 18$, $P = 0.043$) to choose the correct bucket but could not use the other four cues provided (elbow point: $N = 25$, $K = 16$, $P = 0.23$; tapping: $N = 25$, $K = 12$, $P > 0.99$; body orientation: $N = 25$, $K = 11$, $P = 0.69$; gaze alternation: $N = 25$, $K = 13$, $P > 0.99$; see Figure 2). Of the 18 subjects that correctly used the pointing cue, only 5 investigated the outstretched arm before moving to the bucket.
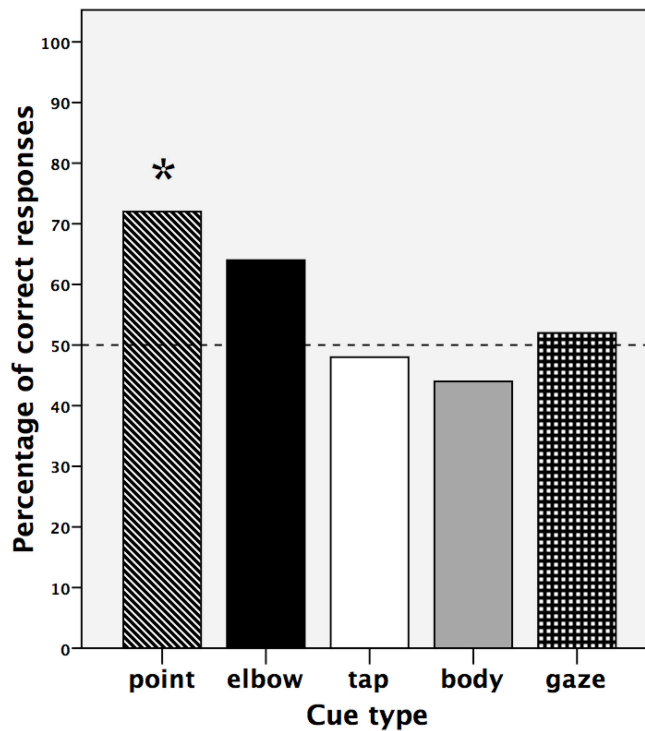
Figure 2. Object choice task. Percentage of correct responses for each cue type. * = $p < 0.05$ (binomial probabilities, two-tailed predictions).

There was no significant difference in the total scores of the 3 age groups ($\chi2_2$ = 1.58, P = 0.45) nor was there any significant differences in individual cue use based on age (point cue: N = 25, P = 0.07; elbow cue: N = 25, P = 0.68; tap cue N = 25, P = 0.88, body cue: N = 25, P > 0.99; gaze cue: N = 25, P = 0.88). Mean scores were: $X \pm$ S.E. = 2.86 ± 0.26 for subjects under 1yr, 2.56 ± 0.29 for subjects between 1 and 2 and 3.00 ± 0.37 for subjects over 2. There was no significant difference in the overall performance of subjects according to size ($\chi2_2$ = 0.83, P = 0.66) nor were there any significant differences in individual cue use based on size (point cue: N = 25, P = 0.74; elbow cue: N = 25, P = 0.16; tap cue N = 25, P = 0.88, body cue: N = 25, P > 0.35; gaze cue: N = 25, P = 0.88). Mean scores were: $X \pm$ S.E. = 2.70 ± 0.37 for subjects under 115cm, 3.00 ± 0.29 for subjects between 115cm and 130cm and 2.67 ± 0.21 for subjects over 130cm). There was no significant difference between the performance of males and females (N_1 = 14, N_2 = 11, U = 69.0, P = 0.64). Overall subjects showed a bias in favour of the bucket on their right

side (N = 125, K = 75, P = 0.031). At an individual level, 6 subjects showed a right side bias and 1 showed a left side bias.

Discussion

Attention attribution task

In the attention attribution task most subjects could use the gross cue of body orientation to determine whether someone was paying attention to them but they could not use the more subtle cues of head direction and gaze. These results are very different from those of adult horses that are highly adept at reading subtle body cues including head direction and eye gaze [13]. This suggests that the ability to read human attentional cues, while present at a relatively early age, becomes refined over time and appears to require significant experience to fully develop. It is possible that attention to body cues may be a general and widespread ability relevant to reading conspecific as well as human cues whereas the attention to head and eye cues may develop in horses as an adaptation to human behaviour. We believe that is it unlikely that the reduced performance of the juveniles is due to a lack of motivation as all subjects were happy to approach the human experimenters and showed no signs of fear. We would also have expected to see an overall reduction in performance rather than a reduction in performance of specific cues if there were attentional or motivational causes. In fact the young horses were highly accurate in their use of the body cue (85%). In this study, however, we did not find a difference in the performance of the subjects according to age. Unfortunately, the relatively small sample size and the effect of different rearing histories are likely to have masked any potential age effects. Thus a more extensive study with subjects from a standardised rearing environment would be of benefit.

This is the first study to date that has looked at attention attribution abilities in juvenile animals and as such it is not possible to directly compare performance in our young horses with other species. As adults, horses appear

to be as skilled as domestic dogs in this task yet this ability seems to take considerable time to develop fully. It is important to note, however, that although some of the young horses in this study are already nearly three years old, many horses are essentially left with minimal training and interaction beyond the provisioning of food for the first year or more of their lives, so even if a relatively small amount of experience with human behaviour is required to learn to use human attentional cues, it may take a number of years for sufficient exposure to occur. In contrast, most very young puppies may well have already had more exposure to human activity than the horses in this study. It would be of interest to attempt to quantify the nature and extent of the interaction between adult and young domestic horses and dogs and their handlers in order to fully appreciate the differences in the relationship they have with humans.

Object choice task

In the object choice task the youngsters performed at a comparable level to adults horses in that they were able to use a distal sustained pointing cue but were not able to use body orientation and gaze cues [14,34]. It is also interesting to note that although not significant, 64% of subjects chose the bucket indicated by the elbow point cue, a cue that may provide weak stimulus enhancement. Neither the juvenile horses tested here nor the adult horses tested by us previously were able to use the momentary tapping cue. It may be that subjects were unable to use the cue because it was removed before the choice was made, however, horses are able to use proximal momentary pointing cues [34]. Alternatively the large arm movements may have discouraged the horses from approaching the bucket – more research is required to explain this response.

There was no effect of age on performance across the task, however, the young horses did appear to be slightly less adept at using the distal sustained point compared to the adults in our previous study (72% vs. 82%). An interesting difference we found between the adult horses we studied previously and the young horses here, was that only 5 of the 17 (29%) young

subjects that used the pointing cue investigated the hand before the bucket whereas in the adult study, 14 of 23 (61%) investigated the hand. This seems to suggest that the young horses had not yet formed a strong association between the human hand and the provisioning of food and that this association may serve to improve performance in these tasks when pointing cues are used. This had also been a factor that has been suggested to contribute the performance of domestic dogs in this task [37].

Although there may be still be some maturation of this skill beyond three years of age, the use of the sustained pointing cue by young horses suggests that its use requires little (or even no) experience of humans to develop. In this task domestic dogs appear to have some appreciation of the communicative intent of these cues whereas adult domestic horses tend to rely on stimulus enhancement, a more basic learning mechanism that is possessed by many species. As such it is perhaps not surprising that this skill appears to be present at a relatively early age. It is also important to note that people, when interacting with horses, rarely attempt to share joint attention. Thus although horses can learn basic pointing cues through learning a relationship between hand and food, they are unlikely to be exposed to attempts to solicit joint attention through more subtle cues such as gaze. Again, a quantitative study of the ways in which people interact with dogs and horses would help us to understand exactly the nature and extent of the cues both species are exposed to in their daily lives.

The ontogeny of the use of human pointing cues has been studied in a number of species. By 8 weeks both hand reared wolves and domestic dogs are able to use proximal momentary pointing [38]. Socialised fox cubs are also able to use a sustained pointing cue regardless of whether they have been selected for tameness, although those selected for tameness were more accurate [39]. Thus the ability of all young animals tested to use basic pointing cues (those that provide a degree of stimulus enhancement) supports the notion that this ability is widespread and develops at an early age. In contrast, the use of distal momentary pointing appears to be a much more complex skill that is acquired by domestic dogs around 2 months of age [29], is not seen in

juvenile wolves, only rarely in highly enculturated adult wolves [6,31,38] and has not been seen in adult horses [34].

General discussion

Our results suggest that the skills required by horses to perform these two human-reading tasks require different cognitive mechanisms with different patterns of development. Adult horses are highly skilled at reading subtle human body cues to determine the direction of their attention and this is a skill that appears to require significant experience to develop. In contrast, horses are not particularly skilled at attending to human communicative cues to choose a rewarded container. They are only able to use cues that provide stimulus enhancement and this skill is present at a relatively early age when horses have not had extensive exposure to humans.

Previous work with dogs has indicated that larger dogs tend to be better than small dogs at using human pointing cues [40]. Larger dogs also tend to discriminate between humans primarily based on facial features whereas smaller dogs tend to discriminate between people based on body cues, suggesting that smaller dogs may also be less able to use facial cues to attention (Osthaus, unpublished data). Clearly horses (even young horses) are generally much taller than domestic dogs, indeed many of our subjects had a whither height that was above the chest height of the experimenter, and in this study we did not find an effect of size on performance. Thus taller young horses were not more able to use the pointing cue compared to smaller subjects and the overall inability of young horses to use head and eye cues does not appear to be due to the small size of some of the subjects.

In this study we found a significant bias in favour of the right side for both tasks. Individually there were also a higher number of subjects with a side bias compared to the adult horses in our previous study. This may be because the young horses found the task more demanding and relied on spatial cues when they were unable to use human gestural cues. It is well know that horses, including foals, readily use spatial cues in learning tasks [41]. It is particularly

interesting however, that they consistently chose the right side. Horses have shown lateral biases in information processing across a variety of tasks, preferring to use their right eye when viewing novel objects but their left when viewing a person [42,43]. Lateralisation has not previously been seen in human cue reading tasks, presumably because in adult horses the side of (some of) the cues, rather than the spatial configuration itself, is the most salient feature of the task. It is therefore not clear what aspect of the task led to a preference for the right side.

The early presence of a skill does not necessarily mean it is innate, nor the late onset of an ability mean it is learnt. We are also aware that the horses in this study were not young foals and had received some exposure to humans but we could not test subjects until they were several months old because we had to wait until they were able to eat food rewards. Subjects were also required to be sufficiently used to human handling that they could be led around the test area and were able to complete the tasks that took on average 10-20 minutes. Despite this, these results strongly suggest that the horses' ability to read human attentional cues is not a skill that appears *de novo*, rather it is a skill that develops through extensive experience over a horses' lifetime. In contrast the ability of horses to use human given-cues that provide stimulus enhancement reflects a general skill that is present early in development in a number of species in which the individuals tested have accepted humans as social partners. Thus the ontogeny of these skills and the proximate mechanisms used by domestic horses appears to be different to that of domestic dogs. By comparing the ontogeny of a wide range of attention reading skills across species we can begin to understand the different mechanisms required for such tasks and the environmental and genetic factors which give rise to these abilities.

Methods

Ethics Statement

The method employed in this study involved interactions that were similar to those the horses were likely to experience in their normal daily routine. Trials were carried out in a familiar setting. The data recorded was observational and non-invasive and as such this study did not require a licence under the United Kingdom Home Office regulations concerning animal research and welfare. This study complied with the University of Sussex regulations on the use of animals and was approved by the School of Psychology ethics committee. No subjects showed signs of stress during the trials.

Subjects

A total of 27 young horses under the age of three participated in this research, 22 subjects completed the attention attribution task (task 1) and 25 subjects completed the object choice task (task 2). Task 1 included 12 males and 10 females, and ages ranged from 6 months to 2.9 years ($X \pm$ S.E. = 1.82 $\pm$ 0.19). Task 2 included 13 males and 12 females, and ages ranged from 9 months to 2.9 years ($X \pm$ S.E. = 1.76 $\pm$ 0.16). Subjects ranged in height from 90cm to 154cm ($X \pm$ S.E. = 121.72cm $\pm$ 3.68 for task 1 and $X \pm$ S.E. = 119.16 $\pm$ 3.59 for task 2). For those that completed both tasks, task order was counterbalanced across subjects. Subjects were from 8 locations and were either privately owned or were from stud farms. Some of these subjects were regularly handled and halter led whereas others had had very little direct contact with humans. Subjects were not food deprived prior to the study.

Procedure

Subjects were tested in an area familiar to them, either an indoor or outdoor school or an outdoor paddock. One young foal that had not yet been

weaned was tested in its own field with its mother and other youngsters and mares in the field held nearby. Trials were conducted between November 2008 and November 2010. Prior to testing, subjects were given a food preference test to see what reward should be given during the trials – choices were between carrots, commercial horse treats and the subjects normal feed. A number of the young horses had small teeth and had never eaten carrots or treats before so were given their normal feed. All experimenters and handlers were female.

Attention attribution task. In this study we replicated the general procedure of Proops & McComb [13] using foals and juvenile horses rather than adults. Subjects were presented with two people, one that was paying attention to them and one that was inattentive. Horses were released to determine whom they chose to approach to receive food.

The experimental set up can be seen in Figure 3. 10 subjects were given a warm up phase in which the experimenters were attentive and 12 were given a warm up phase where the experimenters were inattentive. This was to ensure that the horses were not choosing experimenters in the test phase based on any attentional cues learnt during the warm up phase. It also replicates the protocol of the previous attention attribution study conducted with adult horses. In the attentive warm up, the two experimenters stood at centre point C facing the subject with their hands outstretched together holding a food reward. In the inattentive warm up phase the two experimenters stood at 90º to the subject, facing each other at centre point C with their hands outstretched in the middle of them holding the reward. The handler held the subjects on the left side on a loose lead rope and led them towards the centre point to receive their reward. The subjects were then lead in a semi-circle to the left or the right (the order was counter balanced to prevent side bias) and the procedure was repeated. The experimenters also swapped sides between each warm up trial to reduce the incidence of side biases. The subjects' behaviour was gradually shaped over a maximum of 10 trials so that by the end of the warm-up phase the handler was able to lead to horse to the release

point (R), remove the lead rope and the subject would move forward to the experimenters to receive the reward.

The test phase was the same for all subjects. Four cues were presented to the subjects in a counterbalanced order with an additional reinforcement trial between each test trial. After the warm up phase was complete, the two experimenters moved to points E and adopted either an attentive or inattentive stance. The side of the attentive person, the identity of the attentive person and the side the experimenters stood on was counterbalanced across trials. Horses were not given a reward during a test trial. Once the horse had approached an experimenter in the test trial, the handler collected the subject and the experimenters returned to centre point C. Subjects were led in a semi-circle and rereleased at point R to receive a reward. This reinforcement trial was found to increase the motivation of the subject and improve response rate in adult horses. Subjects were then led in a figure of eight across the test area and held for approximately 30 seconds at point P. This was found to reduce side bias in adult horses. If a horse failed to respond to a cue, a reinforcement trial was given and the cue repeated a total of three times. If the subject still failed to respond to the cue, a recording of "no response" was made and the next cue was presented. Of the 22 subjects, 2 subjects failed to choose an experimenter for three consecutive body cue trials and one subject failed to respond to the eye cue and so they were given a "no response" score for that cue type.

 Four cues to attention were tested:

For the body orientation condition the inattentive person stood with their body turned 180° away from the subject. In the head orientation condition they stood with their body facing forwards but their head turned away and in the eyes closed condition they stood facing forwards but with their eyes closed. During these three trials the attentive person stood facing forwards and maintained eye contact with the subject while keeping their head still. A fourth, mixed condition was included where the attentive person stood with their head facing towards the ground but their eyes looking up towards the subject while the inattentive person stood with their head facing forwards towards the

subject but their eyes looking down towards the ground. Neutral facial expressions were adopted throughout the trials.
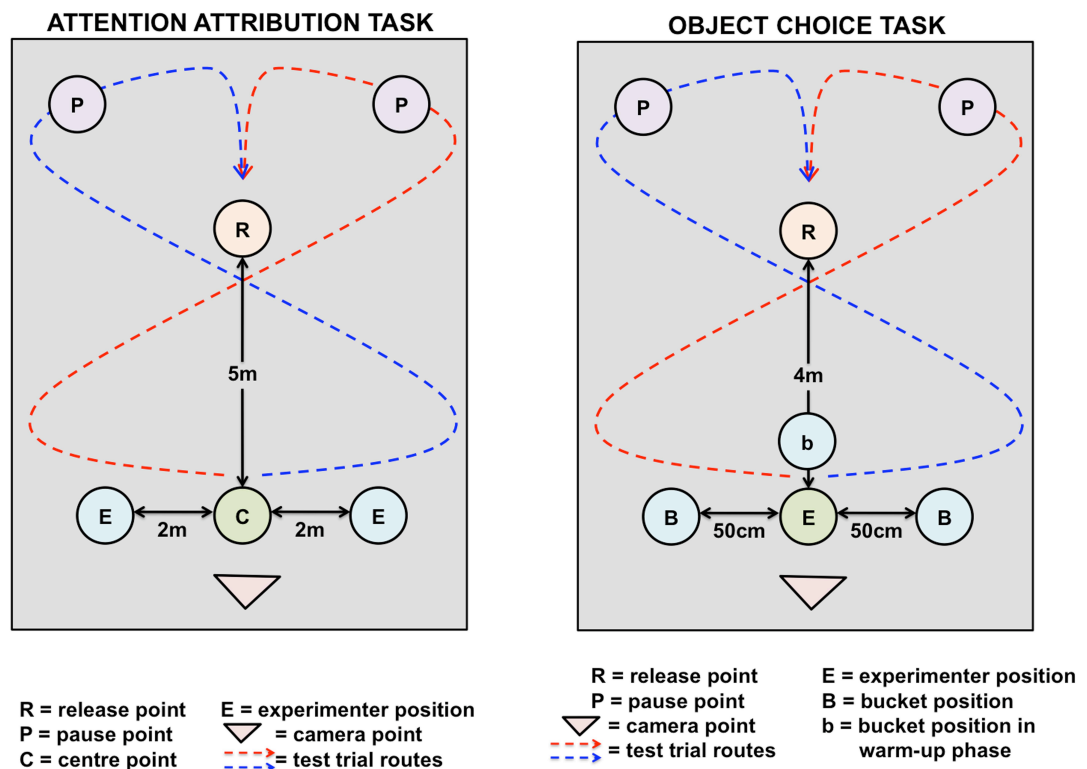
Figure 3. Diagrams of the experimental set-up for a) the attention attribution task and b) the object choice task.

**Object choice task**. In this study we replicated the general procedure of Proops et al [14] using foals and juvenile horses rather than adults. An experimenter cued one of two buckets and subjects were released to determine which bucket they chose to approach.

The experimental set up can be seen in Figure 3. During the warm up phase the experimenter stood at point E with two black buckets (40cm diameter, 19cm height) stacked together in front of them at point b. Food was placed in the bucket and the handler led the subject from the left side on a loose lead rope towards the bucket to collect the reward. The subject was then led in a semi-circle to the left or right and returned to the centre line and was again led towards the bucket to receive the reward. The experimenter swapped the buckets over between each warm-up trial so that each bucket

would smell of the reward. The behaviour of the subject was gradually shaped over a maximum of 10 trials so that by the end of the warm up phase the subject could be released at point R and would walk to centre point C and receive the reward from the bucket.

After the initial warm up phase the experimenter placed the two buckets at points 50cm to the left and right of point E (at points B). As the horse approached the release point along the centre line the experimenter gave one of five cues towards one of the buckets. The subject was then released and if the cued bucket was chosen, a food reward was placed in the bucket as soon as the choice was made. Food was not placed in the bucket prior to the choice being made to prevent sight or odour cues affecting the choice. After the test trial the experimenter returned the buckets to the centre point and the horse was led in a semi-circle and rereleased at point R to receive a reward. This reinforcement trial was found to increase the motivation of the subjects and improve response rate in adult horses. Subjects were then led in a figure of eight across the test area and held for approximately 30 seconds at point P. This was found to reduce side bias in adult horses. If a horse failed to respond to a cue, a reinforcement trial was given and the cue repeated a total of three times. If the subject still failed to respond to the cue, a recording of "no response" was made and the next cue was presented. All subjects responded to all five cues in this task.

The side of the cue was counterbalanced across subjects with half receiving three cues to the left and half receiving three to the right. The side to which the cue was given was pseudo-randomised with the constraint that the same side was not cued more than twice in a row. The order of cue presentation was counterbalanced across trials with each cue being presented first, second, third, fourth and fifth an equal number of times.

Five cues were given:
1.   Distal sustained pointing cue: As the horse approached the release point the experimenter brought her ipsilateral arm out from the side of her body to point towards one of the buckets. This position was held with the body oriented

forwards, looking directly ahead until a choice was made. The index finger was approximately 65cm from the top of the bucket.

2. Elbow point cue: As the horse approached the release point the experimenter brought her elbow out to one side with her hand held on her chest. This position was held with the body oriented forwards, looking directly ahead until a choice was made.

3. Momentary tapping cue: As the horse approached the release point the experimenter reached towards the correct bucket and tapped the side of the bucket slowly three times with large movements of the arm. She then returned to a standing posture, body oriented forwards, looking directly ahead until a choice was made.

4. Body orientation cue: As the horse approached the release point the experimenter turned her whole body towards the correct bucket and stood looking down at the bucket until a choice was made.

5. Gaze alternation cue: Keeping her body oriented forwards, the experimenter alternated the direction of her head and gaze between the horse and the correct bucket until a choice was made.

Behavioural and statistical analysis

Responses were recorded using a Sony digital handycam video recorder and coded by two independent experimenters; there was no discrepancy between the experimenters in their coding of correct and incorrect choices. For the attention attribution task, the dependent variable was whether the subjects correctly chose the attentive person over the inattentive person when determining whom to approach to receive food. A choice was defined as correct if the subject approached the attentive person and stood within 1 meter of the target within 60 seconds of being released. In the object choice task the dependent variable was whether they chose the cued bucket. A choice was recorded as correct if the subject's head approached within 20cm of a bucket within 60 seconds of being released. In most trials subjects touched the chosen bucket but in some cases subjects looked into the bucket without touching it.

In the attention attribution task results from the groups given different warm up phases were compared using 2X2 Fisher's Exact tests. There were no significant differences in the performance of the subjects given the attentive or inattentive warm up phase for any cue type, suggesting that their responses were not conditioned by specific cues given during the warm up phase (body cue: $N = 20$, $P = 0.22$; head cue: $N = 22$, $P > 0.99$; eye cue $N = 21$, $P = > 0.99$, mixed cue: $N = 22$, $P = 0.39$). Results were therefore pooled for further analysis.

The number of subjects in each task choosing the correct target for each trial type was analysed using two-tailed binomial tests. The total number of correct scores was calculated for each subject in each task and effects of sex analysed using a Mann-Whitney U test. The subjects were also divided into 3 age groups (up to 1 year inclusive, up to 2 years inclusive, up to 3 years) and the effect of age on total scores was analysed using a Kruskall-Wallis test. Performance of subjects on individual cues according to age was assessed using 2 X 3 Fisher's Exact tests. We also wanted to ensure that the smaller subjects were equally likely to use the cues provided, particularly in the trials where facial cues were important. To assess whether there was an effect of size, subjects were divided into three size categories: subjects with a wither height under 115cm (roughly up to the height of the experimenter's waistline), subjects 115-130cm (roughly up to the experimenter's shoulder) and subjects over 130cm (subjects above the height of the experimenter's shoulder). Performance of subjects on individual cues according to size was assessed using 2 X 3 Fisher's Exact tests and the effect of size on overall scores was assessed using a Kruskal-Wallis test. Overall side and experimenter preferences were assessed using binomial tests. Fisher's Exact tests were run at the VassarStats website: http://faculty.vassar.edu/lowry/VassarStats.html. All other statistical analyses were performed using SPSS v. 17.0.0 software for Mac.

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DISCUSSION

The research presented in this thesis contributes to the field of comparative social cognition by providing a systematic investigation of socio-cognitive abilities in domestic horses. In this discussion I begin by presenting a review of social cognition in horses which details not just the work I have conducted in this field but also what we know of other areas of social cognition. I then move on to a discussion of what the studies presented in this thesis have told us about the categorisation of conspecifics by animals and the ability of animals to obtain social information from human social partners. Finally I provide a brief overview of how these findings may have contributed to our understanding of comparative social intelligence, how this relates to the social intelligence hypothesis, and I also suggest possible directions for future research.

ARTICLE VI: HORSE SOCIAL COGNITION

(Proops, L. & McComb, K. 2011. In the style of
***Trends in Cognitive Sciences*)**

Summary

The social intelligence hypothesis states that increases in social complexity have driven corresponding increases in relative brain size in primates. The relationship between big brains and social complexity has since been found in other taxa, including ungulates, although the necessary corresponding comparative analysis of social intelligence remains limited to a few species. Here we consider recent findings from a previously neglected study animal, the domestic horse, which provide important new insights into social cognition in mammals. Horses provide an excellent animal model for testing the social intelligence hypothesis because of their complex social lives that have many

parallels to those seen in cercopithecine primates, yet they inhabit a relatively simple ecological environment. We discuss how this new research in the fields of social recognition, reconciliation, social learning, attention attribution and the reading of human communicative cues has furthered our understanding of the mechanisms and evolution of social behaviour.

Introduction

With an evolutionary trend across species, but particularly among primates, for greater brain size, evolutionary biologists and comparative psychologists have sought explanations for this energetically costly increase [1]. One possibility is that the cognitive abilities of animals have developed to fit their particular ecological niche. Correspondingly, evolutionary leaps in brain size within primates, and specifically homonids, are attributed to natural selection favouring individuals able to succeed in increasingly complex ecological environments [2, 3]. However, another factor that often co-varies with ecological complexity within many taxa (including primates, carnivores and birds) is social complexity [4]. Thus an alternative hypothesis that has consistently been accumulating convincing support is the social brain hypothesis, which states that in many taxa the main selection pressure for larger brains is social rather than environmental [5-7]. Those animals within a group that are more able to recognise conspecifics and read their communicative signals, to communicate clearly their intent and form alliances, will be more successful. This selection for social dexterity is believed to lead to increases in relative brain size as a result of the increased processing power required to orchestrate social relationships in large or complex social groups. This relationship between group size or complexity and relative brain size has been found not just in primates [8] but also in other taxa such as the Cetacea [9], Carnivora and some Insectivora [10]. Increases in brain size (and specifically the neocortex) should therefore also correspond to increases in measurable socio-cognitive abilities.

With increasing support for the social intelligence hypothesis, research into comparative social cognition has grown rapidly, and while the number of

species studied within the field is steadily growing, the field continues to suffer from a degree of "apecentrism". More recently domestic dogs (*Canis familiaris*), spotted hyenas (*Crocuta crocuta*) and corvids have also become the focus of considerable research interest as they provide alternative models in which to study the development of convergent human-like social skills and their relationship to complex social systems [11, 12]. However, to fully understand the relationship between large brains, complex societies and social cognition, social intelligence must be studied in a wide range of species – ideally in naturalistic settings. Here we explore the opportunities provided by a new and, until recently, surprisingly understudied animal model – the domestic horse (*Equus caballus*). As an ungulate prey species with a complex social system and a close relationship with man, horses are excellent subjects in which to investigate some of the main fields of interest in socio-cognitive research. We provide the first review of the body of recent research into horse social cognition that has provided some significant insights into the evolution of social intelligence.

The horse as a study species

Horse brains

The study of social cognition in ungulates is its infancy despite recent work suggesting that the social brain hypothesis can indeed be applied to ungulates [13]. Comparative analysis of ungulate species has revealed that evolutionary increases in brain size over time are correlated with increases in sociality [14]. In addition, Perissodactyls (odd-toed ungulates), the order to which horses belong, have seen considerable encephalisation over time, with only primates and cetaceans undergoing greater increases. Specifically, the suborder of hippomorpha which contains only one extant family, the equidae, has undergone particularly large increases in encephalisation compared to other ungulates [15]. Neocortex size in ungulates is predicted not by habitat use or by overall group size but by the complexity of the group, thus species living

primarily in smaller cohesive groups, such as horses, have larger relative neocortex size than species living in large unbonded aggregations [4].

Horses are a good group to study within the social intelligence hypothesis framework because unlike primates and cetaceans, and like many other ungulate species, they have a relatively simple foraging behaviour (ecological environment) but complex social organization and so the effects of the two can be more readily disentangled and assessed. Horses are a species that are not traditionally thought of as intelligent. However, research into the cognitive capacities of horses have tended to focus on basic associative learning mechanisms in the non-social domain, whereas it is likely that any "advanced" cognitive adaptations horses possess will have been driven by social demands. Thus complex cognitive skills are much more likely to be apparent within the social domain in this group [for reviews of equine learning studies see 16, 17, 18] and may be an example of "laser beam" intelligence – in which the abilities of a species is focussed within a specific domain and may not be accessible to the individual nor transferable to other domains [19].

Behavioural ecology

There are two (sub)species of horse, the domestic horse (*Equus caballus*) and the wild Prezewalski's horse (*Equus ferus przewalksii*) and although the vast majority of horses are domesticated and live alongside humans, small populations of wild Przewalski's horses exist as well as a number of populations of free-ranging feral horses. Like many primates, wild and feral horses have an unusual social structure among mammals in that they form year round mixed groups [20]. Individuals live in either bachelor bands or small, largely stable, family bands consisting of a stallion (occasionally multiple stallions) and a number of breeding mares and their offspring [21]. These bands have large home ranges that overlap with several other groups so horses associate to varying degrees with a large number of conspecifics. Occasionally bands will join up with other groups to form much larger aggregations of up to one

hundred individuals, either on a temporary or more permanent basis [22]. As such, horse societies can be viewed as a form of fission-fusion society [23].

Horses are large grazing ungulates that are adapted to life on open grasslands. Although their food is reasonably uniformly distributed, producing a relatively simple ecological environment, their life histories and social organisation contain many parallels with those of other species that are considered to inhabit complex social worlds and possess complex cognitive capabilities. Horses have a long lifespan, with both domestic and wild horses living on average 25-30 years. Although, as prey species, offspring are precocious, they continue to be nursed by their mother for approximately 1 year and remain closely bonded to her until they are driven from their natal band between 3-4 years of age. Out of the breeding season, females tend to instigate group movements and as such, horse societies have been described as matriarchal [24]. Older but not necessarily higher ranking individuals tend to lead group movements suggesting that age and experience are important factors in the successful leadership of horse bands [25].

Like many social primate species, alliances, dominance hierarchies and reconciliation are all important features of horse society. There is a strict usually linear dominance hierarchy within the bands and between the bands in a herd [21]. The more dominant individuals/groups have better access to food, water and shelter. As with many cercopithecine primates and spotted hyenas, rank doesn't necessarily correlate with size, although unlike many primates, both males and females disperse from their natal band and so rank and affiliation are rarely kin based. Like many primates, horses form strong bonds with particular individuals within their group that can last their lifetime and friendships with higher-ranking individuals can provide benefits such as improved access to resources [26]. Stallions may also share the defence of a harem and access to mares with other males, although whether this constitutes genuine cooperation/alliance formation is debatable [27-29].

An important prediction of the social intelligence hypothesis is that individual fitness should be strongly influenced by social dexterity. In baboons (*Papio*

ursinus), females who maintain strong social bonds with other females experience higher offspring survival and increased longevity [30, 31]. Similarly, recent research has shown that female feral horses that develop strong bonds with other unrelated mares in their band have greater reproductive success than individuals that are not so socially integrated. Interestingly, social integration was not based on age or dominance in this case [32]. Thus, social competence appears to be a highly adaptive trait for horses. These apparent similarities in the social organisation of horses and primates and the importance of social bonds, suggests that analogous socio-cognitive skills may have developed to deal with this social complexity. We now review horse social cognition in a number of domains that have been widely studied in primates and/or other species living in complex societies.

Complex social knowledge

How animals categorise others provides insights into the complexity of their social knowledge and how they perceive their social world. By possessing detailed, hierarchically structured mental representations about others that may include, for example, information about rank, affiliation and kinship, social animals are more able to predict the behaviour and interactions of others and act appropriately given a particular social situation. In addition, being able to use the communicative and attentional cues of other group members allows individuals to gain important information about their environment. Related abilities such as recognising individuals, learning from others, reconciliation, understanding what others can and cannot see and using the communicative cues of others have all been extensively studied in primates and recent research is beginning to highlight surprising abilities in horses across these domains.

Recognising others

Cognitive abilities such a having a good memory and being able to recognise social partners are important prerequisites for the development of the kind of

detailed social knowledge that is vital to success in complex societies. The discrimination of kin from non-kin is widespread particularly among parents and offspring but evidence of discrimination between categories of unrelated individuals is less common. Horses reliably discriminate between the vocalisations of group members, neighbours and strangers suggesting that horses, like elephants (*Loxodonta africana*) and primates, possess hierarchically structured information about different categories of social groups [33]. Horses also have considerable long-term memories, remembering discriminative stimuli and conceptual rules such as relative size for over six years [34]. In a social context, observational reports suggest that horses remember previous group members for a considerable amount of time and will reform groups with these individuals within larger herds after a year of separation [35].

Being able to recognise specific individuals is the most fine-grained form of categorisation of others and for humans a significant feature of this ability is that it is cross-modal, allowing us, for example, to match the voice of a known individual to the sight of them. The ability to integrate information from multiple senses was once thought to be a uniquely human ability but it is becoming increasingly clear that animals are also able to use cross-modal information in socially complex ways. Research demonstrating that elephants encountering the scent of a family member on the path in front of them have expectations about their whereabouts and that primates hearing the call of an infant will look towards its mother, clearly suggest that other animals may also be capable of recognising others cross-modally [36, 37]. Recently we demonstrated that an animal – the domestic horse – was indeed capable of cross-modal individual recognition, indicating that this ability is likely to be the mechanism underlying findings such as those highlighted above [38]. See Box 1. Thus complex internal representations such as the concept of a person or individual are likely to be widespread, having evolved in a number of distantly related social species [39].

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BOX 1 - Cross-modal individual recognition of conspecifics
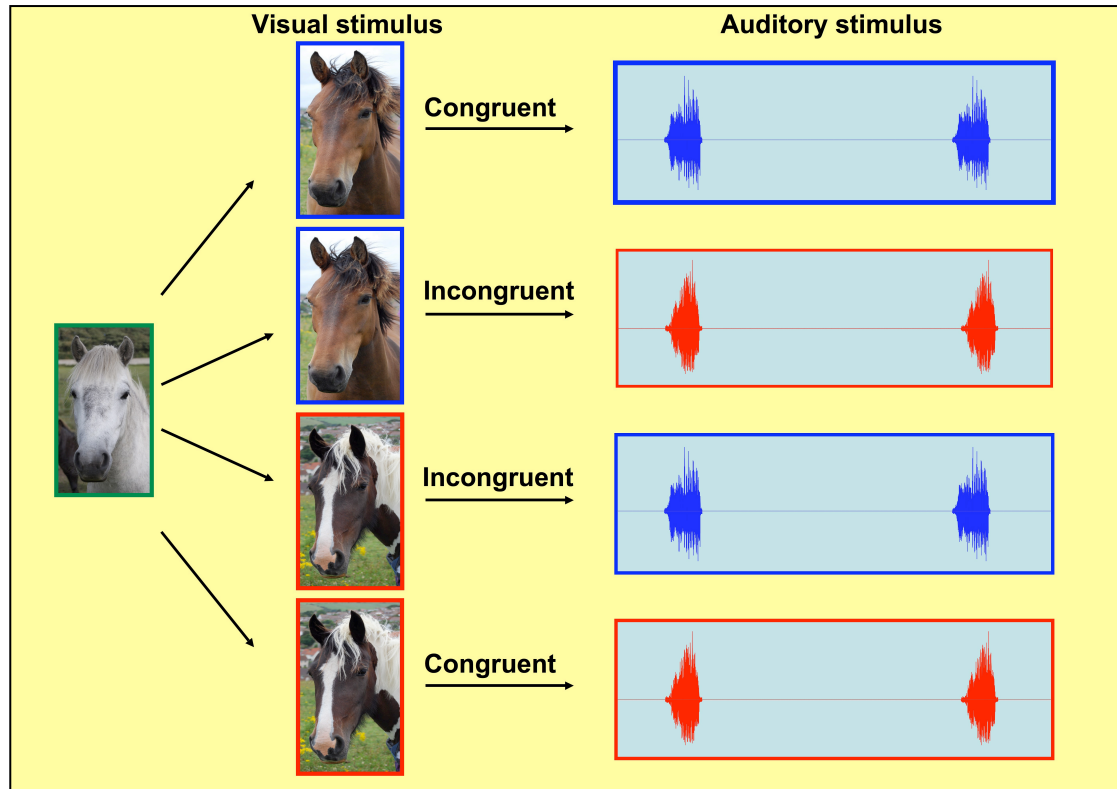
Figure 1. Diagrammatic representation of the experimental paradigm, as applied to one of our 24 subjects.

Our experiment was based on an expectancy violation paradigm where horses were shown a herd mate who was then led past them and disappeared behind a barrier. After a delay of at least 10 seconds, the subjects were played 2 long distance contact calls (whinnies), which were either calls from that associate (congruent trial) or calls from another familiar herd mate (incongruent trial). These calls came from a loudspeaker placed close to the point of disappearance. Each subject participated in a total of four trials (two congruent and two incongruent) as shown in Figure 1. Four horses from our 2 study sites were randomly chosen to be "stimulus horses" (that is the horses that were shown to the subjects) and were presented to 6 subjects each. Each subject received a unique call exemplar for each stimulus horse.

We predicted that if horses were capable of cross-modal individual recognition, the presentation of the first visual cue would activate some form of pre-existing multi-modal representation of that individual, creating an "expectation" that the subsequent vocal cue would correspond to that associate. The subjects would therefore show surprise when they saw a familiar horse but the vocalisation heard was from a different associate. And this "surprise" would be indicated behaviourally by responding more quickly and looking for longer in the direction of the call during incongruent compared to congruent trials. This is indeed what we found.

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For domestic horses, humans also represent significant social partners, allowing us to study the extent to which social knowledge and recognition abilities are adaptable in the types of individuals encoded. Horses tend to generalise their positive or negative experiences with particular humans to their subsequent interactions with other people and remember these associations for a long time, which is an adaptive skill [40]. However, they are also able to learn to discriminate between different individuals on the basis of both body and facial cues and transfer positive or negative associations from photographs to the actual people [41, 42].

We conducted a second series of experiments to determine whether horses spontaneously recognised familiar humans in their day-to-day lives. Again we wanted to determine if individual recognition could occur cross-modally. In the first experiment, horses saw a familiar handler and a stranger standing in front of them. When subjects heard the voice of their handler they looked more often and for longer at this familiar person but they didn't look more at the stranger when they heard the unknown voice. This demonstrates that horses are capable of cross-modally discriminating between strangers and familiar people but they only match the voice and sight of a person if the person is familiar to them. To determine whether horses are capable of cross-modal individual recognition (rather than the more simple task of discrimination between familiar

and unfamiliar individuals) we then presented subjects with the sight of two highly familiar human handlers. Subjects looked preferentially at the person who matched the voice they heard, indicating that they are indeed capable of cross-modally recognising familiar people [43]. This finding shows the potential flexibility of horses' conceptual knowledge by demonstrating that their cross-modal recognition of individuals can extend to morphologically very different social partners to themselves.

Reconciliation

Peacemaking behaviours are adaptive social strategies for closely bonded social groups in which it is important to maintain social cohesion and to repair damaged relationships following intra-group aggression. As such peacemaking behaviours should occur in species with complex, hierarchical, social organisation in which long-term social bonds are important for individual fitness. Individuals must also possess the cognitive skills required to recognise others and remember past interactions with them. Reconciliation (increases in affiliative behaviour between former opponents after a conflict) has been studied almost exclusively in primates but has also been demonstrated in a few other species including ravens, spotted hyena, domestic dogs, bottlenose dolphins (*Tursiops truncatus*) and goats (*Capra hircus*) [for a review see 44, 45]. In addition, increased affiliative behaviour between a combatant (often the victim) and an unrelated individual may occur (third party affiliation) and can take the form of appeasement (a third party displaying affiliative behaviours to the victor), solicited consolation (the victim displaying affiliative behaviours towards a third party) or "true"/unsolicited consolation (a third party displaying affiliative behaviour towards the victim).

Both reconciliation and third party affiliations, including consolation and appeasement, have recently been documented in domestic horses [46]. In this study reconciliation occurred at an intermediate level to that documented across primate species. For horses, third party affiliations were very frequent (occurring after 58.5% of conflicts). Unsolicited or "true" consolation appears to be

relatively rare in primates and does not appear to occur in bottlenose dolphins, yet is seemingly common in domestic dogs, rooks (*Corvus frugilegus*) and ravens (*Corvus corax*) [44-49] and is also likely to be a significant feature of conflict management in horses. The consoling of others, when observed in children and apes, has been attributed to the ability to empathise with the victim [50]. The fact that this form of "true" consolation now appears to occur in phylogenetically distant species, forces us to conclude either that sensitivity to others' emotional states is also widespread or that consolation does not necessarily require cognitively complex mechanisms such as empathic understanding.

Social learning

Social learning refers to the ability of an animal to acquire information from observing others. Social learning allows for the potential acquisition of considerably more knowledge than could be acquired through trial and error learning during an individual's lifetime and is an important precursor to the development of culture. The social organisation of horses, their long lives, and the extended period in which youngsters closely associate with their parents, provides ample opportunities for horses to learn from their associates. Despite this, several studies have tried and failed to show social learning in domestic horses and for a long time it was believed that horses were not capable of learning from others [for a review see 16]. However, in the studies mentioned above, all the demonstrator horses were unknown to the subjects. As outlined previously, in the wild, horses tend to follow leaders that are older, often higher ranking, and presumably wiser than themselves, suggesting that they may well discriminate between individuals that are worth learning from and those that are not. Adult horses have also been found to play an important role in regulating the behaviour of youngsters by reducing aggression rates and increasing social cohesion within groups [51]. This suggests that young horses learn appropriate social behaviour from adult group members, (and emphasizes the importance of housing domestic horses in natural, mixed age groups [52]).

In addition, experiments investigating social learning in horses have generally been based around social feeding tasks. In 3 of the 4 studies conducted previously, young horses were tested with an unknown adult demonstrator horse that they may have seen as dominant [53-56]. It is now clear that when horses are presented with the choice of two places to feed they prefer to return to a previously successful site but will actively avoid this location when a dominant individual has been feeding at this site and remains nearby [57]. Some horses, if they receive a direct threat from a dominant individual in this feeding context, will continue to avoid the site where a dominant individual has fed even when they are out of sight. This may well have caused some of the subjects to actively avoid the location at which the demonstrator horse had fed previously.

Krueger et al [58] devised a task that didn't involve feeding decisions and assessed the effects of social relationships on social learning in horses by providing known subordinate, dominant and unknown horses as demonstrators. The subjects observed the demonstrator horses following a human handler around an enclosure and subsequently, when allowed to interact with the person, only subjects that had observed a dominant horse following the human copied this behaviour. Not only does this show that horses are indeed capable of some form of social learning, it demonstrates that they use social strategies to decide whom to copy. These findings also have important implications for the training of horses and the development of horse-human bonds. Potentially, watching a dominant horse interact well with handlers will "teach" younger horses appropriate behaviour towards humans.

What horses know about seeing

In a similar way to social learning, the ability to detect the direction of a social partner's attention has obvious adaptive advantages by allowing animals to gain important information about their environment. It also provides an opportunity for an animal to engage in more effective communication. Horses appear to follow the gaze of conspecifics, paying more attention to the gaze of dominant

individuals than subordinate or unknown horses [unpublished data cited in 59]. Horses are also very good at knowing whether a person is paying attention to them or not. When presented with two people, one of them paying attention to them and the other inattentive, horses will reliably approach the person who is attending to them to receive a treat. This they can do based not just on the orientation of a persons' body but also on more subtle cues such as head orientation and whether the eyes are open or closed [60].

The ability to detect eye direction and attribute attention in a social context has been considered to be an evolutionary precursor to possessing a theory of mind [61]. There are, however, a number of ways in which an animal may be able to use the attentional cues of others, either through low-level behaviour reading, through a higher-level understanding of mental states or through an intermediate level mechanism involving the representation of rule-based knowledge [62-64]. It is therefore important to establish the mechanisms involved in attributing attention and exactly what an animal knows about another's attentional state. If animals show that they are able to use attentional cues across a variety of tasks in a flexible way and apply their knowledge of attentional states to novel situations then it is argued that this demonstrates that they have at least a knowledge-based understanding of attention that goes beyond simple low level cue-based learning.

To date what horses know about seeing has only been tested in a few contexts. In addition to following the gaze of conspecifics and discriminating between attentive and inattentive humans when choosing whom to approach for food, horses also obey a command more readily when a stranger giving the command is paying attention to them [65]. In this study, horses obeyed the command of a familiar handler regardless of attentional state but were sensitive not only to the body orientation of a stranger but also their eye direction when deciding whether to obey their command. One pilot study has also reported that horses produce more auditory and tactile begging behaviours when a human holding food has their eyes closed or obscured than when their eyes are visible – suggesting that horses have some appreciation of what others can and cannot see and are aware of the importance of gaining another's attention for

communication to be successful [66]. In addition, the fact that horses adjust their attention-seeking behaviour according to attentional state suggests that there may well be a degree of intentionality behind these gestures. Thus horses appear to be highly sensitive to subtle eye cues to attention across all tests to date, demonstrating a flexibility that may be indicative of knowledge that goes beyond simple low-level mechanisms.

Understanding human communicative cues

A significant field of social cognition has arisen over the last decade looking at the ability of animals to read human communicative cues. By looking at these "human-like" skills across a variety of animals researchers can assess the potential analogous and convergent evolutionary factors that may give rise to complex human socio-cognitive abilities [11]. Dogs are highly adept in this domain which has led to the hypothesis that dogs have evolved this ability through selection and convergent evolution during the process of domestication [67]. See Box 2. The domestication hypothesis has yet to be systematically studied in other domesticated animals, however, recently a number of researchers have begun to look at how good horses are at interpreting the communicative gestures of humans.

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BOX 2 - The domestication hypothesis

Domestic dogs are particularly good at reading human communicative gestures in object choice tasks, using a wide variety of cues in a flexible way that suggests they have some understanding of the referential nature of the cues provided. They can also determine when a person is paying attention to them in different contexts by using gross cues such as body orientation as well as more subtle cues such as eye gaze. In contrast the performance of apes and monkeys is often surprisingly poor [for a review see 60, 68].

Research indicating that puppies require relatively little experience in order to use human communicative cues and that dogs outperform hand-reared wolves (*Canis lupus*), suggests that this in an ability that has a strong genetic component that was not inherited from the domestic dog's ancestor, the wolf [69, 70, see 71, 72 for contradictory findings]. This has led to the hypothesis that, due to the close relationship with man, domestic dogs developed enhanced "human reading" skills during the process of domestication [67]. Further support for this hypothesis comes from a project in which a group of silver foxes (*Vulpes vulpes*) were selectively bred for tameness. Within very few generations they underwent morphological changes that made them look more like domestic dogs; their colouration became more varied and white appeared in their coats (a general feature of domestication across species), their tails became more curly and their ears more floppy. In addition, this domestic strain of foxes was as good as dogs at reading human communicative cues whereas the performance of a wild strain was considerably poorer [73]. These results strongly support the domestication hypothesis but also suggest that the enhanced ability of domestic dogs to read human cues may have occurred indirectly via a general selection for tameness. Since tameness is clearly a trait that is highly desirable in all domestic animals, it is possible that the domestication hypothesis can be extended to domestic species in general.

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The standard task is simple. Subjects are presented with two or three containers and a person gives a communicative cue to indicate which is the correct container. A wide variety of cues have been used including body orientation, gaze, marker placement, tapping and several pointing cues including those that are presented near the container (proximal) or at a distance from the container (distal) and those that are given until the choice is made (sustained) versus those that are removed before the choice is made (momentary). To date four studies have looked at the abilities of horses to use human cues in an object choice task.

In the first pilot study with horses, only 4 horses managed to proceed to the test phase and of those four horses, 2 could use a tapping cue and one could use a proximal point [74]. However, the protocol in this study required horses to learn the operant response of turning over a bucket to receive the food whereas subsequent studies have not required training and consequently have had much lower drop out rates. Horses are also able to use humans as a basic local enhancement cue and will choose the bucket where a person is standing [75]. In an extensive study of horses' use of different types of pointing cues, subjects were able to use both distal and proximal sustained pointing cues and a proximal momentary pointing cue but were not able to use a distal momentary pointing cue [76]. We studied horses' abilities to use a variety of other cues and found that they were not able to use gaze (head) alternation, body orientation or momentary tapping cues but could use a marker placement cue, and, as was reported previously, could use a distal sustained point cue [68]. See Figure 2.

Thus overall horses fail to use the distal momentary pointing cue, considered the benchmark for demonstrating cue use that goes beyond simple stimulus enhancement cues and also fail to use other cues such as gaze and body orientation that provide no stimulus enhancement. This pattern of results coupled with the observation that subjects often approach the outstretched hand or marker before investigating the bucket has led researchers to suggest that horses employ basic cognitive mechanisms and have no appreciation of the communicative intent underlying these gestures. It must be noted however, that horses are able to use a proximal momentary pointing cue and do not use a highly salient momentary tapping cue [for possible explanations of this result see 68], findings which are not totally compatible with the hypothesis that horses only use stimulus enhancement cues.

Figure 2. In an object choice task, subjects were presented with containers and a human experimenter provided cues as to which container the subject should choose to receive a reward. In this task, horses were able to spontaneously use some human communicative cues such as distal pointing, but were unable to use other cues such as body orientation and gaze.

One prediction of the domestication hypothesis is that the above skills are relatively hard-wired and require little experience to develop. When we tested 25 juvenile horses aged between 6 months and three years on an object choice task, we found that they were as able as adult horses to use a distal sustained pointing cue and like the adults were unable to use body, gaze and momentary tapping cues [77]. In addition we found no improvement in the ability to use distal pointing according to age. Although enculturation effects cannot be ruled out, these results do suggest that relatively little experience is required for this skill to develop. In contrast, the ability of juvenile horses to read human attentional cues was markedly poorer than those seen in adult horses, with the

youngsters being able to use body orientation but not head or eye movements to choose whom to approach to receive food. Thus this skill may rely more on enculturation during an individual's lifetime. However, 2 year old horses with minimal human contact were less likely to obey a command when the stranger issuing the command was looking away from them than when their attention was directed towards them, thus in this rather different context, young horses were sensitive to subtle eye cues [66]. The differential abilities of the subjects in these two tasks may be due to the different experience of the subjects or may indicate that eye cues are more salient in a task where an unknown person is exhibiting dominant behaviour by issuing commands than when subjects are choosing whom to approach for food. More generally these findings suggest that the development of sensitivity to human attentional cues may be context specific.

Although horses are able to spontaneously use a number of human given communicative cues and are extremely sensitive to human attention, the results presented here do not provide direct evidence that horses possess enhanced abilities to read human cues that are a direct result of domestication. It is very possible that humans have selected for horses that are more adept at using human visual and acoustic cues. However, horses are also sensitive to small intraspecific visual signals and are attentive to heterospecific cues in the wild, thus it is also possible that the skills reported here reflect abilities possessed by both domestic horses and their wild cousins. It is also extremely difficult to compare the performance of different species in the object choice task when subjects have very different rearing histories. Most studies that assess the abilities of apes to read human communicative cues test institutionalised apes that are not representative of their species, they often have traumatic life histories that lead to social and cognitive disruption, no exposure to humans during early development and limited current exposure [78]. In contrast studies of the abilities of domestic dogs usually use subjects that are highly enculturated, having been reared from a very early age within family homes. From a comparison of this research it is impossible to determine the extent to which any observed differences are genetic or learnt. This problem is also faced, to a lesser extent, when we compare domestic horses with dogs

because horses have far less exposure to humans during their lifetime and the nature of their interactions with people are also very different, with many communicative cues occurring when horses are ridden. Closer examination of the mechanisms underlying these abilities coupled with a wider range of tests administered to young subjects, species experiencing comparable rearing environments, and phylogenetically related wild and domestic species would help to elucidate further the evolutionary mechanisms involved in the development of "human-like social skills".

Conclusion

The social intelligence hypothesis states that large brains develop in response to the greater processing demands that arise when individuals live in complex social groups [5-7]. Relative to other ungulates and several other taxa, horses possess large brains and also inhabit a challenging social environment that has many similarities to that of social primate species. In the wild, horses associate to varying degrees with a large number of conspecifics, strict dominance hierarchies exist both within and between groups, young horses appear to learn social skills from adult group members, and individuals form strong bonds with specific unrelated others. Crucially, an individual's social competence appears to have direct consequences for their fitness [32]. In contrast, horses inhabit a relatively simple ecological environment, suggesting that any complex cognitive skills that horses possess are likely to have developed to allow them to survive in their complex social world. In this review we outlined some of the recent research demonstrating that horses are indeed capable of complex social cognition.

Horses are able to recognise social partners across modality and appear to use the knowledge of specific individuals to decide whom to learn from. Studies of reconciliation suggest they employ peacemaking strategies to maintain social cohesion and may even be sensitive to the emotional distress of others. Horses are also highly adept at reading human attentional cues and some human communicative cues, allowing further investigation of the relationship between

domestication and the development of human-like social skills. However, much still remains to be learned in these key areas of socio-cognitive research if we are to fully understand the nature of horse social cognition. See Box 3. Recent studies of horse social cognition have demonstrated that some seemingly complex abilities such as cross-modal individual recognition and reconciliation are likely to be widespread among social species. Findings from other species such as the spotted hyena suggest that complex societies can also evolve without the need for individuals to possess correspondingly complex cognitive mechanisms [79]. Thus horses may be able to achieve similar social behaviour to primates via more simple mechanisms and further analysis of the cognitive mechanisms underlying horse cognition is warranted. In addition, by comparing the socio-cognitive abilities of species with both complex and simple social environments we can begin to determine the degree to which underlying mechanisms are widespread or specialised social adaptations and thus determine what conditions are required for the development of large brains and complex social intelligence [80]. To this aim, the horse provides an excellent model system.

BOX 3 - Questions for future research

- **Social brains:** The family Equidae consists of both highly social species that exhibit female defence polygyny such as horses, and more solitary species that exhibit territory defence polygyny, such as wild asses. Do wild and domestic horses therefore also possess a relatively large neocortex compared to less social, closely related species such as wild asses and domestic donkeys (*Equus africanus asinus*)? If so, do these differences in brain structure correspond to differences in socio-cognitive abilities?

- **Individual recognition:** Just how complex is the social knowledge horses possess about individuals? Clearly horses possess

representations of individual social partners that are independent of modality but do they possess the kind of complex hierarchically structured representations of individuals (containing information such as rank, kinship and affiliation) that is evident in baboons [81]? Do they possess correspondingly rich representations of their human partners? Initial research suggests that horses do have some expectations about how specific familiar humans will behave [65].

- **Reconciliation:** "The valuable relationship hypothesis" states that relationships that afford an individual the most benefit (such as relationships with high ranking individuals, "friends" or mates) should be those relationships that are most sought after and those which individuals most seek to maintain [82]. Do horses, like other social species such as ravens, domestic dogs and some primates assess the value of social partners when determining whom to "reconcile" with and whom to "console" or "appease" [44, 45, 83]? By discovering who consoles whom, and by assessing the stress levels in both victims and third parties during conflict and consolation, we can begin to understand the function of consolation and to discover whether the underlying mechanism involves a form of emotional contagion (in which the third party may seek consolation for their own distress) or whether there is evidence of other forms of empathic understanding.

- **Social learning:** Horses are capable of social learning but the cognitive mechanisms involved are unclear. Is this behaviour a form of generalised stimulus enhancement or does it involve the imitation of specific acts? Is this imitation based on any inference of the demonstrator's intention? It is also adaptive to be discerning when deciding whom to copy and horses appear to preferentially learn from dominant individuals. To what extent are horses sensitive to the knowledge states of others and do group members swap demonstrator and observer roles according to situation and experience? Since the following of a human handler has been described as a form submissive behaviour, does this mean that the observer horses in the study reported above deduce the relative rank of

the human by watching them interact with a herd mate of known rank? In other words, are horses capable of transitive inference, a process which allows animals to infer the relative rank of an unknown individual from their interactions with others, thus reducing the need to test the social status of the stranger directly through potentially costly confrontation? Preliminary studies, lacking an appropriate control, suggest that horses may also be able to learn detour and instrumental tasks from human demonstrators [84]. If horses possess this ability, it would allow for controlled investigations into the cognitive mechanisms involved in social learning by horses and also provide the opportunity to investigate how horses view humans. For example, do horses show similar patterns of social learning from both conspecifics and human handlers? Do they only learn from familiar people and do they perceive their handlers as higher-ranking members of their social group?

- **What horses know about seeing:** Recent studies have shown that horses are highly sensitive to human attentional states and are able to use subtle cues such as eye gaze to adjust their modes of communication and alter their behaviour towards humans. What remains to be determined is what exactly horses know about seeing. Do they make these decisions based on simple associative learning or do they possess, as the current research seems to suggest, a more complex rule-based knowledge of attentional states or even some awareness of the mental states underlying attention? Horses have yet to be tested in highly novel contexts or with other conventional tasks that determine, for example, the extent to which animals understand the effects of barriers to vision and whether they distinguish between knowledgeable and ignorant individuals based on their visual perspective.

- **Understanding human communicative cues:** Although dogs are extremely adept at reading human communicative cues, in other tests of physical cognition, and even tests of social cognition that do not directly involve the use of human communicative cues, wolves and chimpanzees reliably outperform domestic dogs. Dogs may therefore possess a highly

domain-specific ability to read human cues [85-87]. Similarly, horses do not appear to perform well in non-social tasks but show some complex socio-cognitive skills, including in their ability to read human cues. To what extent are horses' cognitive abilities a social specialisation, as the social intelligence hypothesis predicts? On the other hand, to what extent are horse social skills particularly adapted to the reading of human cues, as may be expected by the domestication hypothesis? In addition, the hypothesis that horses have inherited their abilities to read human cues from their wild cousins rather than through the process of domestication has yet to be tested. Direct comparisons of the human-reading skills of domestic horses and their wild and feral cousins as well as comparisons between horses and other closely related wild and domestic species that have more solitary social systems, such as asses and donkeys, would provide further insights into the effects of domestication on equid species.

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In the article above I reviewed recent research that has provided important new insights into horse social cognition across a variety of fields. In the final sections of the discussion I move on to examine how the results presented in this thesis have furthered our understanding of animal social cognition in general. As with the introductory and main sections of the thesis, I separate the discussion of my results into two research areas, experiments exploring the discrimination and classification of social partners and experiments exploring horses' ability to obtain information from human social partners. Lastly, I discuss my findings within the context of the social intelligence hypothesis and draw some final conclusions.

DISCRIMINATION AND CLASSIFICATION OF SOCIAL PARTNERS

The "concept" of individual

The ability of horses to spontaneously recognise familiar individuals using multi-modal identity cues, as demonstrated in Articles I and II, indicates that animals are capable of forming some kind of integrated, higher-order representation of social partners that is independent of modality and is therefore not based on the matching of perceptual stimuli. In this way it has been argued that horses possess what we would call the concept of an individual, "raising intriguing questions about the origins of conceptual knowledge" (Seyfarth and Cheney 2009). Humans and horses last shared a common ancestor about 125 million years ago, implying that the ability to form complex representations of individual social partners is likely to have evolved in a number of social species via the process of convergent evolution. Cross-modal individual recognition has now also been shown in grey-cheeked mangabeys (*Lophocebus albigena*) and rhesus macaques (Bovet and Deputte 2009; Sliwa et al. 2011). Systematic investigations of cross-modal individual recognition, not only in other mammal species but also in birds, and potentially reptiles and fish will help to determine just how widespread this ability is. In

addition, domestic horses often have largely solitary lives or live in social groups that frequently change in composition. By studying the cross-modal recognition abilities of horses that live in different social situations we can also determine how robust this ability is and how much experience of other individuals is required to recognise them. The findings for such research could also have important welfare implications for the housing of domestic horses.

Following on from our research presented here, it would now be of interest to determine just how rich horses' concepts of individuals are. Complex social behaviour involving alliance formation, friendly grooming, reconciliation and fight interference have all been reported in horses (Feh 1999; Waring 2003; Cozzi et al. 2010). The extent to which the social cognition underlying these behaviours of horses is as complex as that reported in other species such as primates should now be addressed by attempting to determine how much knowledge horses acquire about other individuals. It is also necessary to determine how they categorise relations between these individuals, for example, by discovering if horses, like baboons, simultaneously encode information about the dominance status and kinship of familiar conspecifics (Seyfarth et al. 2005).

Methods developed to study conceptual knowledge in pre-verbal infants have proved to be extremely useful in the study of information acquisition in animals (Cooper et al. 2003). For example, the expectancy violation paradigm allows researchers to investigate whether animals can hold mental information and use it to determine future events. Behavioural responses indicating "surprise" when presented with anomalous rank interactions or, in the case of Article I, incongruent combinations of cross-modal identity cues, suggest that animals possess concepts such as "dominant" or "individual" and detect a violation of expectation based on stored memories when sensory cues presented do not correspond to these stored representations (Seyfarth et al. 2005). These methods can be used to investigate further the structure of conceptual knowledge in horses and other animals.

Adaptability of the individual recognition system

Article II of this thesis provided an investigation into the extent to which the cross-modal recognition ability of horses is adaptable and can be employed to identify human social partners. It is well known that humans and primates (and probably many social species) become naturally specialised to attend to the identity cues of conspecifics. In the first few months of life human infants are as capable of discriminating between the auditory, visual and cross-modal identity cues of other species as they are between cues to human identity. However, through the process of perceptual narrowing, these skills become specialised in the discrimination of human cues and specifically the identity cues of people from the same ethnicity (Cheour et al. 1998; Pascalis et al. 2002; Lewkowicz and Ghazanfar 2006; Kelly et al. 2009; Pons et al. 2009). Primates have also been shown to be more skilled at discriminating conspecific faces and cross-modal identity information than heterospecific cues (Pascalis and Bachevalier 1998; Adachi et al. 2006; Dufour et al. 2006). However the period of sensitivity to heterospecific cues can be extended in human infants via exposure to another species (Pascalis et al. 2005), and in primates, an improved ability to discriminate humans can also be achieved through extensive early exposure to people (Sugita 2008; Adachi et al. 2009).

These results point to the fact that discriminatory abilities can be flexible and that experience during an individual's lifetime will affect the species and types of other individuals they are able to distinguish. What our findings demonstrate is that sensitivity to heterospecific cues can be extended to enable animals to perform what may be the most complex of social discriminations, that of cross-modal individual recognition of another species. Recent research has shown that rhesus macaques are also capable of cross-modal recognition of familiar human handlers. However, there is some evidence that the morphological similarities between humans and other primates may facilitate recognition across these species and more limited flexibility in the recognition system may be required to encode identity information here (Taubert 2009; Sliwa et al. 2011). In contrast, Article II of this thesis clearly confirms that complex

recognition systems can be highly adaptable in the identity information that they can encode by demonstrating that an animal – the domestic horse – is capable of encoding cross-modal identity information about familiar individuals with very different physical characteristics to themselves. What remains to be determined is exactly how widespread and versatile this ability is across different animal species.

The neural bases of individual recognition

Conceptual knowledge of a particular individual combines and goes beyond the physical properties of the category and contains functional information that allows for correct categorisation in novel contexts. Modern imaging techniques are allowing us to understand more about how conceptual knowledge is stored in both humans and animals, revealing clear homologues suggesting an evolutionary continuity of conceptual systems. Traditional views of the human conceptual system as a discrete module of symbolic/linguistic units are now being challenged by neurophysiological evidence suggesting conceptual systems are more universal and consist of widely distributed, multi-modular circuits (Barsalou 2005). The findings from Articles I and II, that horses can recognise individuals across sensory modalities supports the view that complex multi-sensory processing is widespread among species.

Although the precise neural basis of such concepts as "the individual" have yet to be determined, it has been suggested that areas of the primate association cortex represent identity information conceptually by combining information from different sensory modalities, coupled with semantic and episodic memories of that individual (Barsalou 2005; Campanella and Belin 2007). When a conspecific call is heard, corresponding areas across sensory, motor, emotional and association areas of the brain are activated, suggesting that corresponding information learnt previously regarding the sight, taste, smell, emotional relevance and how to interact with the individual are activated, presumably to allow predictions about the current situation (so called "situational pattern completion"). This neural circuitry in monkeys closely resembles the circuitry

associated with the representation of conspecifics in humans (Gil-Da-Costa et al. 2004). The process can easily be envisaged as occurring during the expectancy violation and preferential looking tasks outlined in this thesis, where seeing a familiar individual would produce corresponding activity in areas related to the sight and sound of that individual as well as producing associated emotions and corresponding motor activation that drives either escape or approach behaviour. Our findings therefore suggest that this form of multi-sensory representation of individuals underlies individual recognition systems and may well be found across a wide variety of species.

In addition, the recognition abilities of horses when presented with heterospecific identity cues in Article II, showed pronounced hemispheric specialisation. Subjects were able to readily identify individuals cross-modally when visual cues were presented in the right visual field and responses almost dropped to chance when these cues were presented in the left visual field. While this is the first study of lateralisation during the spontaneous cross-modal recognition of individuals, the results are consistent with previous indications of a left hemisphere bias in the processing of multi-modal information during matching-to-sample tasks (Gaffan and Harrison 1991; Delfour and Marten 2006), supporting the hypothesis that the left hemisphere is involved in template matching and the discrimination between relevant and distracting stimuli (MacNeilage et al. 2009; Rogers 2010). In contrast, voice-face processing in humans and face processing in primates and sheep appears to be under control of the right hemisphere (Kendrick 2006; Campanella and Belin 2007). However, horses have been shown to rely more on global body cues than facial cues when discriminating between people (Rossiter 2006). Thus it may be that when facial features drive recognition the specific face processing centres in the right hemisphere are selectively activated whereas recognition based on more global cues may rely on other functional areas of the brain in the left hemisphere.

When both humans and sheep view faces, right hemispheric activation is followed by subsequent increases in left hemispheric activation (Seeck et al. 1997; Peirce and Kendrick 2002). It has been suggested that the right

hemisphere is responsible for the initial processing of identity information and the assessment of novelty versus familiarity whereas the left hemisphere may be involved in the more top-down retrieval of memories and details associated with specific individuals (Rhodes 1985). Our research outlined in Article II is different from most other research into hemispheric specialisation in that it investigates the retrieval of information about genuine social partners associated with long-term relationships rather than arbitrary voice-face pairs learnt in lab-based studies. By presenting horses with facial cues to the identity of familiar individuals, we could alternatively test the hypothesis that cross-modal recognition involving voice-face pairs preferentially activates the right hemisphere in a species other than humans. Comparisons between possible asymmetries in discriminatory ability when voice-face pairs are learnt artificially compared to when the stimuli represent known individuals for whom the subjects presumably possess rich and complex memories, would also help to clarify the role of the left hemisphere in the retrieval of details associated with well-known individuals. Moreover, replication of these studies in other species would help determine the prevalence of these functional cerebral asymmetries.

The orienting responses of subjects towards the voices of familiar handlers showed a weak asymmetry towards turning to the right whereas there was no evidence of lateralisation of responses to the unknown voice. Although further work is required to confirm these tentative findings, they suggest that familiar and unfamiliar human voices are processed in different ways by horses. What remains to been determined is the extent to which the recognition of familiar conspecifics is controlled by the same mechanisms as those controlling the recognition of familiar heterospecifics. These initial findings (that responses to familiar humans but not unfamiliar humans are lateralised) support the neurophysiological data from sheep suggesting that familiarity with human social partners can produce changes in the encoding of visual identity stimuli that results in patterns of activation analogous to those seen when sheep view conspecifics (Kendrick 2006).

It is clear that the discovery of a left hemisphere bias in the discrimination of cross-modal individual identity cues in horses has produced as many questions as answers and further studies of this ability in other species coupled with measurements of corresponding brain activity will be required to elucidate the precise mechanisms involved in the task. It is also important to confirm the relationship between overt behavioural asymmetry and asymmetrical cortical functioning, as this not always straightforward (Fischer et al. 2009; Teufel et al. 2010).

OBTAINING INFORMATION FROM SOCIAL PARTNERS

Results from Articles III-V have shown that horses are highly sensitive to subtle human cues in certain circumstances, such as attributing attention to others, but demonstrate less impressive abilities when using human cues to locate hidden food. In addition, the role of ontogenetic factors appears different in these two tasks, with attention attribution skills appearing to require considerable experience to develop whereas the ability to use simple human communicative cues appears to be present at a relatively early age. In this section I discuss what these results indicate about the proximate cognitive mechanisms involved in these two tasks and how these may differ from those found in other species. I then move on to discuss the possible ontogenetic and phylogenetic factors that may give rise to such skills and the extent to which the findings support different explanations of animals' abilities to read human cues. In addition I provide suggestions for future research that would further elucidate the processes involved in understanding human social partners.

Cognitive mechanisms

Results from Article III demonstrate that horses are sensitive to small bodily cues when determining whether people are paying attention to them, including the visibility of the eyes. In this study horses have therefore proven to be as sensitive to human attentional cues as domestic dogs and have outperformed

many primates tested. Eyes, or schematic representations of eyespot patterns, evoke anti-predator behaviour in many species and the intensity of an animal's reaction to approaching humans can depend on both the direction of head and the visibility of eyes (e.g. hognose snakes (*Heterodon platirhinos*) Burghardt 1991; black iguanas (*Ctenosaura similis*) Burger et al. 1992)). It is presumed that this type of behaviour is triggered by a simple reflexive eye detector mechanism yet the ability to detect eye direction and attribute attention in a social context has also been considered to be a precursor to possessing a theory of mind (Baron-Cohen 1994; Povinelli and Eddy 1996; Ferrari et al. 2000; Itakura 2004). These very different interpretations of attention attribution highlight the importance of determining the underlying cognitive mechanisms involved in understanding another individual's postural and communicative cues.

The question of what is going on in the mind of an animal during a social interaction is a difficult one, and discussions of animals' understanding of human behaviour feed into the broader debate between low level, behaviourist explanations and higher, more cognitive explanations. While some researchers believe that the evidence suggests that mental state attribution is a strictly human ability (Povinelli & Barth, 2005) others believe that apes at least have some capacity to attribute intentions and belief to others (Tomasello et al., 2005). A medium level explanation in regards to chimpanzee social cognition has been suggested whereby apes are capable of understanding the communicative nature of behaviours and are able to use complex contextual rules without actually being aware of mental states (Call, 2001). Since animals can only attribute mental states to others through observing their behaviour it is extremely difficult to determine whether an animal is reading behaviour or reading mental states via behaviour by using some form of higher order representational process. Many researchers argue that if an animal can display sufficient flexibility of behaviour and an awareness of the pertinent factors in social interactions then they are showing a skill that goes beyond simple associative learning (Miklosi and Soproni 2006). Thus if an animal is able to comprehend a variety of communicative or postural signals and this comprehension is relatively independent of context, it is argued that some form

of knowledge about the communicative nature of the behaviours has been acquired.

To date very little work has been conducted to look at attention attribution skills in horses and it is therefore very difficult to determine how flexible these skills may be. However, recent studies do appear to show that horses are sensitive to subtle human attentional cues across a variety of contexts. For example, when horses are trained by a familiar person to obey a command ("stay") they will obey that command regardless of the handler's attentional state. However, if the command is given by a stranger, horses are much more likely to disobey the command if the stranger has their back turned or is not looking directly at them (based on eye direction alone) (Sankey et al. 2011). One pilot study has also reported that horses produce more auditory and tactile begging behaviours when a human holding food has their eyes closed or obscured than when their eyes are visible – suggesting that horses do have some appreciation of what others can and cannot see and are aware of the importance of gaining another's attention for communication to be successful (knowledge that goes beyond simple eye detector mechanisms) (Takimoto and Fujita 2008). Of course, whether they have acquired this through behaviour reading and associative learning or whether they have any appreciation of the underlying mental states behind attentional differences is unclear. While trainers often advise handlers not to stare directly at a horse since this could be viewed as an aggressive act, our research suggests that horses are able to distinguish between a look of friendliness and a threatening look. It would be of interest to investigate this further by determining how sensitive horses are to the contexts in which gazes are given. This would also help determine the flexibility of horses' knowledge of human postural cues and the underlying intent.

Following on from this finding, a systematic investigation into the ability of horses to interpret human emotional cues would also be of interest. Although there is considerable interest in looking at the evolution and interpretation of emotional signals across primates, there has not been a corresponding investigation into the possible convergent evolution of emotion reading skills in domestic animals. Even the domestic dog has yet to be systematically tested.

Anecdotally, horses are well known for their sensitivity to human emotional states. Correlations have been found between the attitudes of handlers and both the corresponding heart rate and behaviour of handled horses, such that horses handled by people with a negative or fearful view of horses showed more anxious behaviours and had elevated heart rates (Hama et al. 1996; Chamove et al. 2002). The effects of short-term changes in human anxiety levels have also been assessed in a study in which people were asked to lead or ride a horse between two points. On the fourth pass, the handlers/riders were told that an umbrella would be opened. Although this did not occur, there was an increase not only in the heart rate of the human but also a corresponding increase in the heart rate of the horse (Keeling et al. 2009). Although the precise cues horses use to pick up on the anxiety of humans have yet to be investigated, increased lead tension has been found to be related to certain behaviours indicating arousal in the horse (Chamove et al. 2002).

In contrast to the results from the attention attribution task which suggest horses may have some form of rudimentary understanding of the relationship between seeing and knowing, the limited use of cues in the object choice task suggest that in this situation the communicative intent underlying the behaviour is not understood. Thus horses fail to show the flexibility of cue use seen in domestic dogs and some other species, such as dolphins. However, if the standard object choice task was taken to be the definitive measure of an animal's ability to comprehend the referential nature of communicative cues, both dogs and horses would possess socio-cognitive skills that were far superior to many primates. This is clearly not the case, and although primates typically perform extremely poorly in object choice tasks, in other potentially more complex and direct tests of mental state attribution, apes appear to have some awareness of the intent underlying communication, for example, by distinguishing between intentional and accidental acts (Hare et al. 2001; Call et al. 2004; Tempelmann et al. 2011). To gain a full appreciation of the extent to which horses are sensitive to the knowledge states underlying the production of communicative and postural cues, horses will need to be tested in other related tasks. Such tests could include an assessment of whether horses distinguish between

knowledgeable and ignorant conspecifics or humans. Pigs have been shown to follow knowledgeable conspecifics to feeding sites and these knowledgeable pigs have also been shown to adapt their behaviour to avoid being exploited by others - waiting until the other pig is put of sight before approaching the feeding site (Mendl et al. 2010). There is currently no strong evidence that dogs distinguish between conspecific and human "Knowers" and "Guessers" (Cooper et al. 2003), and conflicting evidence as to whether dogs distinguish between rational and irrational acts (Range et al. 2007; Hauser et al. 2011; Kaminski et al. 2011). In contrast, ravens and scrub jays are acutely sensitive to the knowledge state of potential pilferers and ravens are also sensitive to the intentions of human experimenters when cacheing food (Bugnyar and Heinrich 2005; Dally et al. 2006; Bugnyar et al. 2007; Bugnyar 2011). However, there are currently no comparable tests in horses.

In addition, subtle behavioural measures must be more readily incorporated into studies of social knowledge. Research measuring eye gaze or hesitancy rather than more overt responses has shown that monkeys are sensitive to eye gaze in a begging task (Hattori et al. 2007), that dogs are more sensitive to whether a person is not attending to them in a fetching task (Gácsi et al. 2004), that seals are sensitive to the difficulty of cues in an object choice task (Scheumann and Call 2004) and that young children know more about the false beliefs of others than they can overtly display (Southgate et al. 2007). Our study of attention attribution also found that horses were slower to respond to head and body cues when they were making the wrong decision, indicating that the horses had some awareness of uncertainty, a form of metacognition, and that their implicit knowledge of attentional cues may be greater than overt responses suggest.

The potential role of ontogeny and phylogeny

As outlined in the introduction, several hypotheses have been put forward to explain the differences in the performance of species across tasks involving the use of human-given cues. Essentially these theories emphasize either phylogenetic factors, including the potential effect of domestication, or they

emphasize ontogenetic factors. Clearly the factors influencing an individual or species' ability to read human cues combines both these causes to varying degrees and in this section I review what our results suggest about the development of human reading skills in horses and how these findings impact on broader theories of human reading skills.

The recent interest in the extent to which animals can read human-given cues stems from the finding that domestic dogs are particularly adept in this domain. This has led to the subsequent conclusion that the skill was acquired through convergent evolution during the process of domestication. The further suggestion that this skill evolved indirectly through a general selection for tameness indicates that, all things being equal, other domestic animals should also have undergone similar selection pressures, leading to the development of this skill. The fact goats, with minimal human contact, unlike many apes, can use tapping and proximate pointing in an object choice task is seen as partial support for the domestication theory (Kaminski et al. 2005). Therefore in much the same way, our findings that horses are very good at reading human cues to attention and are able to use some human communicative cues without the need for any direct training may also suggest that domestication has selected for this skill. However, there is no strong indication that this ability reflects anything more complex than the discrimination of stimuli via basic learning mechanisms.

The domestication hypothesis suggests that experience should have little effect on performance (Udell et al. 2010a). Horses perform as well as dogs in an attention attribution task but the results from Articles IV and V show that it takes horses over three years to reliably learn to use the more subtle cues to attention when deciding whom to approach for food. In contrast, horses as young as 2 are able to use eye cues to determine a person's attentional state when determining whether to obey a stranger's command (Sankey et al. 2011). This suggests that horses are able to use subtle human attentional cues from an early age in certain contexts (perhaps those that are functionally important and have obvious parallels with conspecific cue use in the context of aggressive or

dominance interactions) but considerable experience is required to refine this skill and apply it across a variety of contexts.

In object choice tasks horses perform less well than dogs and it is possible that this is because they lack the relevant experience with people. The environment horses are kept in is generally more comparable to that of shelter dogs than dogs living in human homes and there is now some evidence that dogs living in shelters (a situation also more directly comparable to primate subjects housed in primate centres) may perform poorly on tasks involving reading human communicative cues (Wynne et al. 2008; Udell et al. 2010b). Although horses' limited ability to use certain basic human communicative cues in an object choice task appears to be present at an early age, requiring little experience to develop fully, their ability to use human communicative cues does not appear reach the level of sophistication seen in dogs.

Udell et al (2010a) propose a two-stage hypothesis to explain an animal's sensitivity to human behaviour. To be adept at reading human cues, a species/individual must firstly be able to accept people as social partners and this will depend on the extent to which a species is plastic in the individuals it bonds with during its sensitive social period of development and the amount of exposure to humans it receives during this time. Dogs have a much longer sensitive period in which they can bond with humans than wolves but we know very little about the possible critical periods of socialisation in domestic horses and whether these are different to those seen in wild equids. However, within this framework horses may be more amenable to accepting human partners than primates and will probably have had more exposure to humans than most primates during this sensitive period of socialisation. In contrast, horses may be less predisposed to accept humans as social partners than domestic dogs (due to differences in canid and equid ancestry and/or differential effects of domestication) and undoubtedly would have less exposure to humans during this early socialisation period. During the second stage of the process cue use is learnt through conditioning and again horses are likely to have more opportunity to learn human cues through their daily interactions than apes kept in institutions but probably less opportunity than dogs.

In addition, by virtue of their size, the nature of the communications between humans and horses is very different from that between humans and dogs, with much of the interaction either occurring while the person is standing to one side of the horse or while the horse is ridden. My experience with both dogs and horses also suggests that we regularly attempt to solicit joint attention with dogs and direct them to external objects such as food or toys, but this sort of interaction is not common with horses. A systematic analysis of the nature of communications and relations between humans and dogs and humans and horses (and indeed captive primates and humans) would help elucidate the role of learning. This should also include detailed observations of natural interactions with very young puppies reared in the home or with a litter because the extent of the communication and the number of human postural cues they are exposed to may be considerable.

The other group of hypotheses outlined in the introduction emphasize the natural predispositions of wild animals and the extent to which these may impact on a species' ability to read human cues (e.g the canid generalisation hypothesis, competition-cooperation hypothesis and emotional reactivity hypothesis). It is possible that horses are predisposed to attend to the subtle postural cues of conspecifics and naturally attend to the behaviour of heterospecific members of mixed herds, thus facilitating their ability to read such small human cues (Goodwin 1999). One obvious way to further assess the role of domestication and of traits inherited from wild ancestors would be to compare the abilities of domestic horses with those of their wild cousins in much the same way as has been done with domestic dogs, wolves and silver foxes. Practical constraints have hindered this endeavour and novel and innovative techniques will be required to make such comparisons. However, I think it could be possible to at least capture young feral horses (e.g. mustangs) and raise them in the same way as domestic foals to see if there is any appreciable difference in their responses to humans. While these horses have been domesticated, they have had several generations to revert to their wild-type. Observations of the nature of the bonds formed between humans and both domestic and wild equids as well as their performance on standard tests of

human-reading skills would provide insights into the evolutionary changes undergone by domestic horses.

Similarly, equids have two types of social organisation, Type I typified by female defence polygyny is seen in feral and wild horses and Type II, resource defence polygyny, is seen in wild asses (Linklater 2000). As such domestic horses evolved from ancestors with complex societies in which social bonds were vital for survival and domestic donkeys evolved from a more solitary species in which the only consistent and stable relationship was between mother and offspring. Given this difference it would be interesting to compare the abilities of these two species to bond with heterospecific social partners and read their behavioural cues. However, differences in the section pressures experienced during domestication may also play a role in any variation observed.

Many of the hypotheses that have been proposed to explain the differences observed across individuals and species in their abilities to read human cues remain very difficult to evaluate. Very few studies have adequately controlled for previous experience to allow differences to be attributed to evolutionary factors. By testing a wide variety of both closely related and disparate species across different tasks and, crucially, providing detailed observations of the nature of the relationships and experience animals have with humans, we can begin to elucidate the factors that give rise to an ability to understand human action. This thesis provides a first step in attempting to address these questions in the domestic horse, by demonstrating that, by the time horses are adult they have become highly sensitive to human attentional cues and although they readily use basic human cues to locate food, they fail to use more referential gestures. Attempts to directly compare horses with other species given comparable rearing histories are required before any firm conclusions can be drawn as to the role of phylogenetic and ontogenetic factors in the development of this skill.

SOCIAL BRAINS AND SOCIAL COGNITION

It is clear from the Articles presented in this thesis that horses are capable of some seemingly complex social cognition, including the ability to determine the direction of another's attention and cross-modally recognise individuals both from their own species and also a morphologically very different species. However, to further our understanding of social cognition in horses as well as other species and to more directly test the social intelligence hypothesis I propose the need for research in 4 key directions:

a) Since elements of complex social organisation can be achieved via simple cognitive mechanisms, attempts should be made not just to correlate social organisation with encephalisation but socio-cognitive complexity with encephalisation. The comparison of proximate cognitive mechanisms used by different species to achieve the same social goals would be required.

b) Following on from this, it is important to counterbalance the interest of scientists in assessing seemingly highly complex social skills (and comparing animal abilities with that of humans) by focussing more on cognitive similarities in very basic learning mechanisms that may underpin seemingly much more complex social behaviour.

c) In addition direct assessment of the specificity of cognitive abilities within a species could be attempted by administering controlled comparable social and non-social tasks given within the same experimental framework.

d) Finally, a more balanced approach to the choice of species investigated could be achieved by studying the cognitive complexity of more non-social species, enabling a more robust test of the social intelligence hypothesis. Advocates of the social intelligence hypothesis have tended to focus on social species and the complexity of their social cognition, while negative results from non-social species are also required to confirm the hypothesis that social complexity drives increases in cognitive complexity.

I deal with each of these points below:

The social intelligence hypothesis has been criticised for being vague with respect to producing testable hypotheses (Dunbar and Shultz 2007) and although controlled phylogenetic studies comparing social organisation or ecological environment with brain development have been made, corresponding controlled comparisons between social and non-social *cognitive* skills and brain size have yet to be performed. One of the primary goals of comparative psychology is to construct "cognitive phylogenies" (Fitch et al. 2010). Within this framework it would be necessary to determine just how cognitively complex the mechanisms underlying observed abilities are and then map these skills onto taxonomic trees to determine which mechanisms are widespread, which are shared by a limited number of species through analogous evolution and which developed a number of times across clades through the process of convergent evolution. Thus it is important to determine for example, whether horses' ability to use eye cues to detect attention reflects an innate predisposition to attend to subtle changes in stimuli through simple associative learning or whether the mechanism involves some appreciation of the mental state underlying attention. Similarly, although cross-modal recognition was once thought to be a uniquely human ability, the work presented here and that of modern neuroscientists working in this area suggests that this skill may be widespread and based on what now could perhaps be considered a fairly universal mechanism. Species with seemingly complex social organisation such as horses may be successful in tests of social cognition using mechanisms that are less complex than those observed in other socially complex species such as primates. This case is clearly illustrated by the extensive work conducted by Holekamp and colleagues looking at social cognition in hyenas (Holekamp et al. 2007). Hyenas have complex fission-fusion societies that are very similar to that observed in many primates species; they form clans of approximately 50 individuals, they recognise individuals via multiple sensory cues, and they recognise third party kin and rank relationships which they use adaptively in making social decisions such as when to attack individuals or come to their aid (Engh et al. 2005; Holekamp et al. 2007). Hyenas also have a relatively large neocortex, and although the findings from

studies of hyena social cognition generally support the social intelligence hypothesis, Holekamp et al (2007) conclude that hyenas employ less complex cognitive mechanisms to achieve similarly complex social behaviour to primates, relying more heavily on "social facilitation and simple rules of thumb".

Findings such as the demonstration of gaze following and social learning in solitary red-footed tortoises (*Geochelone carbonaria*) not only highlight the fact that non-social animals may be equally as able, given sufficient experience, to perform social tasks as social species, but also that seemingly cognitively demanding tasks may be achieved through simple associative learning (Wilkinson et al. 2010b; Wilkinson et al. 2010a). Since the 1970s, comparative psychologists have tended to place an emphasis on seeking evidence for "higher-order" cognitive processes, such as theory of mind, in order to compare such abilities to those found in humans. However, recent research has suggested that many human abilities themselves may be determined by relatively simple and unconscious mechanisms. It is therefore important to look not just for differences in highly sophisticated cognitive abilities but also for similarities in very basic learning mechanisms that may underpin much more complex social behaviour (de Waal and Ferrari 2010; Shettleworth 2010). The focus would then change from determining which species possess a specific ability to discovering how this skill is achieved and what evolutionary and ontogenetic factors are required. By demonstrating, for example, that horses are capable of cross-modal individual recognition, we have shown how abilities once thought to be uniquely human, the ability to recognise individuals and synthesize multi-sensory information, are more widespread and are likely to rely on basic neural mechanisms with a long phylogenetic history.

In addition by comparing socio-cognitive complexity with cognitive complexity in non-social tasks we can begin to determine the extent to which social problems have indeed driven increases in cognitive processing in horses. This is a comparison lacking across all species studied, although a few attempts at providing controlled comparable social and non-social tasks have been made with dogs and primates. For example, in an object choice task, dogs were found to rely more on human communicative cues whereas apes relied more on

causal cues such as the container making a noise when shaken. Based on these findings the authors suggest a dichotomy between the "causal ape" that is adapted to a complex foraging environment and the "social dog" that is adapted to life as a human companion (Brauer et al. 2006). A further study suggests that the enhanced social skills of dogs may be restricted to situations involving communication and cooperation with human partners. Given a social and non-social reversal learning task, dogs performed poorly on both tasks, whereas chimps were significantly better at the social task (Wobber and Hare 2009). Similar studies of horses would provide the first real insights into the extent to which the cognitive abilities of horses are domain specific.

Although there are no direct comparisons of horses' ability to perform comparable social and non-social tasks, the demonstration of complex socio-cognitive abilities such as cross-modal individual recognition, is in stark contrast with studies of equine learning and concept formation in a non-social context where performance is typically poor and lacking in flexibility (Nicol 2002; Murphy and Arkins 2007). For example, in a non-social context there is conflicting evidence about whether horses are able to keep track of the whereabouts of hidden food for 10 seconds and their generally poor performance has led to the suggestion that, as obligate herbivores, horses are able to remember the location of food patches but their delayed response abilities are poor and are likely to reflect a lack of prospective memory for events (McLean 2004; Murphy 2009). However, our results from Article I clearly show that horses are able to keep track of the whereabouts of associates for the time between them moving behind the barrier and their calls being played (at least 10 seconds), thus, in a social context at least horses are able to recall past events to predict future events. It must also be noted, however, that the poor performance of horses in some classic learning tasks may reflect the type of stimulus provided or the employment of a methodology not appropriate to the species. For example, horses are particularly sensitive to spatial cues and perform well if reversal learning tasks have a spatial element and poorly if they rely on the reversal of colour cues (Nicol 2002). This further highlights the need for ecologically relevant and directly comparable assessments of social and non-social cognitive tasks.

Finally, in conjunction with direct comparisons between social and non-social tasks within species, corresponding direct comparisons between closely related social and non-social species should also be conducted. Studies of social cognition have tended to focus on species with complex social lives, such as domestic horses, however, it is equally important to test for abilities related to social interactions in non-social species. A few noteworthy exceptions have actually called the social brain hypothesis into question, such as the comparable performance in object choice tasks of social and non-social birds and social and non-social marine mammals (Pack and Herman 2004; Scheumann and Call 2004; Schloegl et al. 2008; Tornick et al. 2010). With regards to equids, it would be of interest to compare the social and non-social abilities of the more social species displaying female defence polygyny, such as domestic horses, with the abilities of the more solitary species displaying territory defence polygyny such as asses.

FINAL PERSPECTIVES

"The social complexity hypothesis predicts that, if indeed the large brains and great intelligence found in primates evolved in response to selection pressures associated with life in complex societies, then cognitive abilities and nervous systems with primate-like attributes should have evolved convergently in non-primate mammals living in large, elaborate societies in which individual fitness is strongly influenced by social dexterity."

Holekamp et al (2007) p. 523

In the introduction I outlined how horses possess a complex social organisation, suggesting that the considerable evolutionary encephalisation seen in equids may have been driven by social demands. In addition, recent research has confirmed that the strength of social bonds in female horses has a direct impact on their fitness. What has yet to be determined is the extent to which horses possess correspondingly complex socio-cognitive skills. Thus the aim of this

thesis was to explore the cognitive abilities of horses across a number of social tasks, with the findings indicating that horses may well be highly socially intelligent. Moreover, all the methods employed in this thesis assess spontaneous behaviour in an ecologically valid situation providing a strong indication of the functional significance of these abilities.

Specifically, we have shown that horses are capable of cross-modal recognition of both herd members and human handlers. These results suggest that this ability may well be widespread and can be employed to encode identity information about morphologically very different heterospecific individuals. Horses also appear to be highly sensitive to human cues to attention and are able to spontaneously use some basic human communicative cues, raising interesting questions about the role of domestication and enculturation in understanding human-given cues. Taken together these results indicate that horses are able to obtain important and detailed social information from both conspecific and human social partners. Moreover the findings clearly illustrate the potential for studies of cognitive abilities in horses to provide unique new insights into the relationship between large brains, social complexity and social intelligence.

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