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Gaze sensitivity: function and mechanisms from sensory and cognitive perspectives

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ABSTRACT

Sensitivity to the gaze of other individuals has long been a primary focus in socio-cognitive research on humans and other animals. Information about where others are looking may often be of adaptive value in social interactions and predator avoidance, but studies across a range of taxa indicate there are substantial differences in the extent to which animals obtain and use information about other individuals' gaze direction. As the literature expands, it is becoming increasingly difficult to make comparisons across taxa as experiments adopt and adjust different methodologies to account for differences between species in their socio-ecology, sensory systems and possibly also their underlying cognitive mechanisms. Furthermore, as more species are described to exhibit gaze sensitivity, more terminology arises to describe the behaviours. In order to clarify the field, we propose a restricted nomenclature that defines gaze sensitivity in terms of observable behaviour, independent of the underlying mechanisms. This is particularly useful in non-human animal studies where cognitive interpretations are ambiguous. We then describe how socio-ecological factors may influence whether species will attend to gaze cues, and suggest links between ultimate factors and proximate mechanisms such as cognition and perception. In particular, we argue that variation in sensory systems, such as retinal specialisations and the position of the eyes, will determine whether gaze cues (e.g. head movement) are perceivable during visual fixation. We end by making methodological recommendations on how to apply these variations in socio-ecology and visual systems to advance the field of gaze research.

Keywords: cognition; gaze following; gaze aversion, gaze sensitivity; retina; visual fixation; visual fields

INTRODUCTION

Attending to where others are looking may offer important information about the location of food and predators, as well as social relationships between conspecifics. Humans employ gaze sensitivity in many contexts: we can accurately follow where others are looking in space (e.g. Bock et al. 2008), and appreciate that others may have different fields of view or perspectives. We use our own gaze as a form of communication to inform or mislead others, and use the gaze of others to interpret their mental states (e.g. Teufel et al. 2010).

A number of other species including mammals, birds and reptiles have also been reported to show sensitivity to gaze. Sensitivity to gaze can result in many different responses, such as avoiding gaze because it is associated with the approach of a predator, or co-orientating with another's gaze to spot objects of interest. Behavioural and sensory ecologists have sought to determine the socio-ecological contexts in which gaze sensitivity occurs, and to identify features of cues which are most important for eliciting gaze sensitivity responses (e.g. Burger et al. 1991; Hampton 1994; Watve et al. 2002; Carter et al. 2008). Numerous experimental paradigms have also been developed to test whether these responses are simply reflexive, and therefore bound to one stimulus in one context, or whether they involve further information processing (e.g. Bugnyar et al. 2004; von Bayern & Emery 2009a; Loretto et al. 2010). The study of this information processing has been of great interest to cognitive psychologists (e.g. Povinelli & Eddy 1996; Call et al. 1998). Many tasks have been designed to identify the cognitive mechanisms by which information from another's direction of attention is processed, and whether these mechanisms allow subjects to apply gaze information flexibly in different contexts, and/or through different behavioural responses. As a result, a plethora of experimental paradigms have been developed to address gaze behaviours in a multitude of different species and contexts.

The aim of this review is two-fold. The first goal is to present a standardised set of nomenclature which brings together all aspects of gaze research (gaze preference, gaze

following and gaze aversion), and defines these behaviours independently from cognitive mechanisms. We hope that this nomenclature brings clarity to the gaze sensitivity literature, and facilitates a bridge between various aspects of gaze research across many disciplines. The second goal is to illustrate how socio-ecological pressures and proximate anatomical, sensory and cognitive factors can influence the occurrence of gaze sensitivity across taxa. These factors can vary substantially between species, and as the breadth of species studied in gaze contexts increases, it is important to consider this variability when interpreting results, designing gaze sensitivity experiments, and choosing appropriate study species.

DEFINING GAZE BEHAVIOURS

A number of different gaze behaviours have been described in the literature and, as a result, this has brought a sense of confusion because many species are studied in different contexts and some definitions carry with them an assumption of the underlying cognitive processing. For example, an animal may orientate their gaze with another individual because they understand the referential nature of looking, i.e. that another individual can *see* something. Alternatively, an animal may orientate their gaze in response to another individual's gaze because having done so in the past resulted in seeing an interesting object. These two scenarios are guided by different processes (discussed in more detail below), but elicit the same observable behaviour. It is therefore useful, particularly in non-human research where mental processes are difficult to ascertain, to describe gaze behaviours purely in terms of the observable behaviour. The terminology used should be independent from any assumptions about the cognitive processes, be it a reflexive response, or one which requires further information processing (see Thornton & Raihani 2008 and Thornton & McAuliffe 2012 for similar arguments concerning the definition of teaching). This is particularly useful in a field where multiple disciplines study gaze sensitivity. For those studying underlying cognition, experimental paradigms can be applied to specifically test

information processing mechanisms underlying gaze behaviours (as defined below). Here we present nomenclature derived from the literature which we propose be restricted to the following definitions.

Gaze Sensitivity

We propose that all instances whereby an individual attends to gaze stimuli should be classed under the umbrella category of gaze sensitivity. Sensitivity to gaze is a pre-requisite for all gaze response-behaviours defined below. Whether an individual is sensitive to the gaze of others may be dependent on a number of factors which are discussed throughout this review, including sociality, ecology, cognition and visual architecture. Gaze sensitivity is also dependent upon the gaze cues available.

Gaze cues

Gaze sensitivity and the resulting gaze behaviours are reliant on an observable gaze cue. Gaze cues include the presence or orientation of the eyes or head, and may be presented as static or moving stimuli. The head and the eyes can be presented in alignment (congruent), or in opposing directions (incongruent), and may also be relative to body positioning. Direct gaze (Fig. 1a) refers to an individual's gaze directed towards another individual, whereas averted gaze refers to an individual's gaze directed away from another individual. Direct and averted gaze can refer to the cues given, but may also be described as gaze responses (e.g. an individual averts their gaze in response to direct gaze, Fig. 1b). In some cases gaze cues and responses occur between conspecifics, or between heterospecifics (e.g. human demonstrator presenting cues to an animal subject, or a predator presenting cues to an animal subject). We now describe gaze behaviours typically observed in response to gaze cues.

Gaze responses

Gaze sensitivity can result in a number of different gaze responses. These include gaze preference, gaze aversion and gaze following responses. Gaze preference refers to an individual's preference for looking at a particular gaze cue. For example, an individual may spend more time looking at another individual that is looking towards them (direct gaze) than one that is looking away from them (averted gaze), or vice versa. Gaze aversion refers to aversive behaviour in response to the presence of gaze cues. For example, an individual moving away from another individual that is looking towards them. Gaze following refers to the act of orientating one's gaze in the direction of another's gaze (Fig. 1c). For example, one individual moves its head to look to the side, and in response, a second individual moves its head in a similar direction. Gaze preference, gaze aversion and gaze following can be further subdivided within these responses (Fig. 2).

Gaze preference

Gaze preference responses refer to looking behaviour from the subject. When presented with a choice between demonstrators exhibiting different gaze cues, an individual may spend more time looking at an individual showing a preferred gaze cue. Gaze preferences may also result in shorter latencies for spotting individuals in a crowd displaying particular gaze cues. For instance, Tomonaga & Imura (2010) showed that when an adult chimpanzee was presented with a screen of many human faces, the subject was faster at detecting a face with direct eye gaze than a face with averted eye gaze. When presented with only one demonstrator, gaze preference may be directed to a specific area of the face such as the eyes rather than the head in general. The demonstrator and the subject may engage in mutual gaze, where both individuals look at one another (Fig. 1a).

Gaze aversion

In gaze aversion, the possible behaviours may be reliant on the context in which the gaze cues are presented. A sudden appearance or approach of gaze cues can elicit aversive escape responses, generally associated with anti-predator responses such as fleeing, crouching or tonic immobility. Similar responses such as fleeing or looking away may also occur between conspecifics, for instance between individual territory holders, or within dominance hierarchies. Gaze aversion can also include behaviours in which an animal is approaching, as opposed to when it is moving away. We refer to aversive approach if a gaze cue is directed towards a desired object such as food, and the subject alters its behaviour by delaying its approach, or approaching only when the gaze cue is averted or hidden.

Gaze following

In gaze following, individuals may orientate their gaze in the same direction, but this does not imply they are necessarily looking at the same thing. In its simplest form, gaze following refers to the co-orientation of gaze with another towards a similar point in space (Emery 1997). Following Emery (1997; 2000), we distinguish gaze following from joint attention. In the latter, an individual not only orientates their gaze in the same direction of another's, but as a result, both individuals' gaze are directed towards the same object (Fig. 1d). This does not suggest that those engaging in joint attention must appreciate the visual attention of others. Further testing would be necessary to pinpoint the cognitive mechanisms (see below). As well as orientating one's gaze with another, an individual may need to re-position itself to be in the same line of sight as the demonstrator. In geometric gaze, an individual repositions itself around a barrier to follow the gaze of another individual (Fig.1e). Geometric gaze may result in joint attention if both individuals subsequently gaze at the same thing behind the barrier.

(Please insert Figure 1 and Figure 2 approximately here)

This terminology serves to bring together all aspects of gaze research. Behaviours such as gaze aversion and gaze following are often studied separately (but see von Bayern & Emery 2009a), yet are inter-related in that they rely on/are based on animals' responses to gaze cues. Therefore it is useful to use the term gaze sensitivity when discussing responses to gaze cues in a broad context, and useful to use the additional behavioural definitions when discussing more specific responses to gaze. Our nomenclature describes the basic components of gaze tasks in terms of behaviours without assumptions about unobservable underlying mechanisms. Once behavioural responses have been observed and categorised, tests can be designed to tease apart the underlying processes which guide these behaviours (c.f. Thornton & Raihani 2008; Thornton & McAuliffe 2012). For instance, do individuals consider where another individual's direction of attention is focused? Might they recognise that another individual's line of sight may be different from their own? Can they use another individual's gaze to infer that individual's intention towards an object? Are individuals able to use gaze flexibly by applying different behavioural responses or cognitive mechanisms across different contexts (e.g. to detect predator gaze, to follow conspecific gaze to find food, and to find predators), or are they bound to one particular response in one particular context? An individual's gaze response may also be dependent upon the availability of gaze cues and their characteristics. For instance, some species may be more sensitive to head direction because they move their head more than their eyes when scanning for or fixating on objects. Alternatively, some species may gain more information from the eyes than the head. Species differences in gaze cues available (e.g., rate and/or orientation of eye or head movement) are highly dependent upon the configuration of the animal's visual system.

Carefully designed experiments allow us to 1) determine how the sensory system of a given species gathers gaze information and 2) establish the cognitive requirements for different gaze behaviours. These proximate mechanisms may help to explain why we see variation in gaze following and gaze aversion behaviours across species. It is equally

important to consider ultimate mechanisms, namely socio-ecological factors which will determine whether attending to gaze cues is beneficial to the observer. Variability in socio-ecological pressures may in fact drive species to process gaze cues such that they can be applied across various contexts. Because this may also be a function of the species' underlying cognition and sensory system, we expect proximate and ultimate mechanisms of gaze sensitivity to be linked, and therefore should be studied in concert.

SOCIO-ECOLOGY AND CUE INFORMATION

Consideration of socio-ecological factors is essential to understand the selective pressures driving the evolution of different forms of gaze sensitivity behaviours. Moreover, socio-ecological considerations also provide critical information into the proximate basis of gaze sensitivity. We expect sensitivity to gaze to occur only if cues are discernible and provide useful information on which the observer can act. Therefore there is often interplay between socio-ecological contexts and the features of the gaze cues available. For instance, predator detection may be dependent on the salience of the predator's eyes, or the prey's capacity to perceive the gaze cues of a heterospecific. There may be a selection pressure for predators to evolve less conspicuous eyes, or to evolve visual configurations that are different from their prey species, making detection of predator gaze more difficult. Similarly, experiments testing for gaze sensitivity often differ in their use of heterospecific (human, predator) or conspecific demonstrators, which may affect whether the subject is motivated to attend to the demonstrator (Emery et al. 1997; Tomasello et al. 1998; Bugnyar et al. 2004; Bräuer et al. 2005). Therefore socio-ecology can give insight into the underlying mechanisms which facilitate the occurrence of gaze behaviours.

Gaze cues from predators

A predator's gaze may give prey species accurate information about the necessity of escape. By accurately assessing where a predator is looking, species may ultimately benefit from increased foraging opportunities (Carter et al. 2008) or more frequent nest visits (Watve et al. 2002). Risk perception may be influenced by the properties of the gaze cue provided by the predator, such as the positioning of the head or eyes, and the colour, shape and size of the eyes (Scaife 1976a; Coss 1979; Jones 1980; Burger et al. 1991). Enhancing or presenting contradictory cues can help experimenters isolate important stimuli for aversive escape responses. Sparrows, *Passer domesticus*, fly away most when a human model is facing towards them, but attend only to head orientation rather than eye orientation (Hampton 1994). Black iguanas, *Ctenosaura similis*, for example, move away sooner when a human face is visible, rather than covered with hair during approach (Burger & Gochfeld 1993). Similar increases in vigilant behaviours are found when the eyes are made to appear larger (Burger et al. 1991). Two eye-like stimuli horizontally placed side-by-side elicit the most fearful responses in jewel fish, *Hemichromis bimaculatus*, (Coss 1979), while in domestic chicks, *Gallus gallus,* the pairing of an iris with a pupil-shape (i.e. having the features of an eye) increases aversive responses (e.g. freezing, distress calls, number of approaches) (Jones 1980) in comparison to other spot arrangements such as no iris or only one eye. However, when testing small passerine predator's preference for invertebrates, there is evidence to suggest that any conspicuous shape, such as a square or triangle on the wings of moths, may be as effective as eye-shaped spots in deterring predation. (Stevens et al. 2007).

Gaze cues that elicit fearful responses may also be important if an animal must approach an object or area where a dangerous agent (e.g. unfamiliar human or predator) is gazing. The conflict paradigm tests whether the subject attends to the orientation of the experimenter's head or eyes by measuring an animal's latency to approach a desired item such as food. If subjects refrain from approaching the food for some time this suggests they are fearful of the experimenter and potentially regard them as a threat. If the subject is

attending to gaze, the latency to approach is expected to be longest when the experimenter is looking towards the object (e.g. Carter et al. 2008; von Bayern & Emery 2009a). This paradigm has mainly been tested on birds, perhaps due to their vigilant, flighty behaviour in the presence of a dangerous agent (typically a human experimenter) alongside their willingness to approach food. Green bee-eaters, *Merops orientalis*, approach their nest sites less (Watve et al. 2002) and starlings, *Sturnus vulgaris*, (Carter et al. 2008) are less likely to approach food sources when a human experimenter is looking. Jackdaws, *Corvus monedula*, show similar responses to starlings, but only if the experimenter is unfamiliar (von Bayern & Emery 2009a). Starlings and jackdaws attend specifically to eye orientation of a different species, not just head orientation.

Assessing a predator's gaze is likely constrained by distance effects, which reduce visual contrast and thus limit the ability to perceive subtle cues (Fernández-Juricic & Kowalski 2011) such as gaze. Individuals may need to get closer to a predator to determine its gaze direction, which could increase predation risk. Consequently, we would expect that sensitivity to predator eye gaze would be more likely in species with high visual acuity (i.e. large eye size relative to body mass, presence of a fovea) as they would be able to resolve at farther distance variations in predator behaviour without incurring too much risk.

The studies cited above examine differential responses to head or eye movement between heterospecifics (i.e. between the subject and the predator or unfamiliar human), but there are also instances of aversive responses between conspecifics. Chimpanzees, *Pan troglodytes*, (Hare et al. 2000) and common marmosets, *Callithrix jacchus*, (Burkart & Heschl 2007) prefer to approach food that a dominant individual does not have visual access to. However, the gaze cues available between conspecifics may not reflect the cues available between heterospecifics (i.e. prey and predator). For instance, chimpanzees and common marmosets may be less sensitive to information from the eyes of conspecifics than humans are, perhaps because many primates have morphological features thought to conceal gaze direction (i.e. dark or no exposed sclera) (Kobayashi & Kohshima 1997; Kobayashi &

Kohshima 2001; Tomasello et al. 2007). Characterising the features of a species' sensory system is necessary in determining what gaze cues are available between conspecifics and heterospecifics.

Gaze cues from group members in predator detection

Information about potential predation risk may be gained not only from the predator itself, but also from the gaze of other group members. Many theoretical models of predator avoidance in monospecific and heterospecific groups assume that collective detection is behind the transfer of information between individuals about potential predator attacks (e.g. Lima 1987). One possibility is that this transfer of information may also occur through gaze following. When animals are farther away in a group, they orient their heads more towards group mates possibly to gather information (Fernández-Juricic et al. 2005). Studies on primates (Tomasello et al. 1998), birds (Loretto et al. 2010; Kehmeier et al. 2011), goats, *Capra hircus*, (Kaminski et al. 2005) and the red-footed tortoise, *Chelonoidis carbonaria*, (Wilkinson et al. 2010) show that individuals follow the gaze of conspecifics looking up, suggesting they attend to conspecifics as a means to detect aerial predators. Following group-member look-ups may be particularly important for animals that forage by grazing or pecking on the ground. Direction of attention would be divided between food sources (on the ground), predators (e.g. on the horizon or in the sky), and possibly conspecific behaviours (e.g. vigilant look-ups). The necessity of relying on conspecific gaze to detect predators and the availability of information from group members will depend on the animal's visual field. Species with larger visual fields may be able to spot predators when their head is down, while other species may need to look up in order to scan for predators (Fernández-Juricic et al. 2004).

We have described two aspects of gaze sensitivity which may function in predator avoidance. Both gaze aversion and gaze following behaviours have been reported across a

broad spectrum of taxonomic groups, from primates to turtles, and it has been suggested that gaze sensitivity may have been present in a common vertebrate ancestor (Fitch et al. 2010). However, we note that few studies have yet to investigate predator gaze sensitivity (but see Stevens et al. 2007), for instance, whether predators prefer to approach prey with averted gaze rather than direct gaze. It also remains unclear whether within-species gaze sensitivity is a prerequisite to between-species gaze sensitivity, and whether gaze aversion is a prerequisite to gaze following, or if they are all independent processes. Studies which consider the visual architecture of a species, and apply a variety of paradigms to the same study species using conspecifics and heterospecifics will help decipher whether gaze preference, gaze aversion and gaze following involve the same proximate mechanisms, and whether they evolved dependently or independently.

Social contexts of gaze following

Individuals may gain information from group members by co-orientate their gaze with others, and many species including all great apes (Bräuer et al. 2005), macaques, *Macaca mulatta*, (Emery et al. 1997), rooks, *Corvus frugilegus*, (Schmidt et al. 2011) and ravens, *Corvus corax*, (Bugnyar et al. 2004) have been reported to adjust their head direction to match that of a demonstrator. To establish whether individuals are in fact taking into account another individual's visual perspective (as opposed to, for example, behavioural coordination of head movements) experimenters have used the geometric gaze task. In this task, subjects must re-orientate themselves so they are in line with another individual's field of view, rather than stopping at the first object in sight (i.e. the barrier) (Povinelli & Eddy 1996; Tomasello et al. 1999). One interpretation is that geometric gaze may be useful for species that conceal information or attempt to obtain hidden information from conspecifics. Geometric gaze has been demonstrated in all five great apes (Tomasello et al. 1999; Bräuer et al. 2005), in spider monkeys, *Ateles geoffroyi*, and capuchin monkeys, *Cebus apella*, (Amici et al. 2009),

domestic dogs, *Canis lupus familiaris*, (Bräuer et al. 2004), and in ravens (Bugnyar et al. 2004). In contrast, Northern bald ibises, *Geronticus eremita*, (Loretto et al. 2010) and gibbons, *Hylobates spp. and Symphalangus syndactylus*, (Liebal & Kaminski 2012) did not gaze behind barriers, indicating that this behaviour is not as widespread as basic gaze following, nor can it be explained by phylogeny as lower apes do not show geometric gaze, while some monkeys do (however, see sensory caveats with regards to gaze sensitivity below). Primates living in competitive social groups may conceal information, for instance, by withholding food calls (e.g. Hauser 1992) or concealing extra pair copulations (le Roux et al. 2013). Gibbons live in small monogamous family groups which may reduce the necessity to conceal actions by group members, although occasional extra-pair copulations have been reported (Sommer & Reichard 2000). The importance of concealment of visual information could be tested by studying geometric gaze in primate species where same-species individuals may vary in their social dynamics (e.g. male bachelor groups vs. family groups). Other lineages known to conceal information from conspecifics include the corvids; therefore, geometric gaze following may be particularly relevant when engaging in caching and pilfering behaviours (Bugnyar et al. 2004; Schloegl et al. 2007).

Some food-caching corvids have been reported to withhold visual and auditory information from potential pilferers (e.g. Bugnyar & Kotrschal 2002; Dally et al. 2005; Stulp et al. 2009; Shaw & Clayton 2012; Shaw & Clayton 2013), or gain visual information from cachers by preferentially watching conspecifics that are caching, as opposed to conspecifics engaged in non-caching behaviours (Grodzinski et al. 2012). In a caching paradigm with ravens, a subject observed a human cache two items, while a demonstrator raven was visible to the subject during both caching events, yet had visual access to only one caching event due to the positioning of a curtain. When given the opportunity to pilfer before their competitor (the demonstrator), subjects preferred to retrieve the food item that was cached when the competitor had visual access, and had no preference when the competitor had no visual access (Bugnyar 2010). Although these studies did not test behaviour specifically in

response to gaze cues, they highlight the importance of a competitor's line of sight during caching and pilfering. Determining if ravens use gaze cues to find food has been explored explicitly using the object-choice task (Schloegl et al. 2008a; Schloegl et al. 2008b).

In the object-choice task, a subject must find food hidden in one of two locations, often under cups or behind barriers. A demonstrator looks in the direction of where the food is hidden, and subjects may attend to the direction of the experimenter or conspecific demonstrator's gaze to determine where food is hidden (e.g. Call et al. 2000; Schloegl et al. 2008a). Ravens were unsuccessful in the object-choice paradigm regardless of whether the demonstrator is a conspecific or a human (Schloegl et al. 2008a). Rhesus macaques and capuchin monkeys were also unsuccessful in the object-choice task when presented with human gaze cues, though capuchins and some macaques choose above chance when given pointing cues (Anderson et al. 1995; Anderson et al. 1996). Chimpanzees also typically perform poorly, perhaps because the experiment is presented in a cooperative framework (Hare & Tomasello 2004). Chimpanzees are accustomed to frequent competition with group members for access to food (e.g. Hauser et al. 1993; Hare et al. 2006), and may not use altruistic, communicative gaze cues. Modifications to the object-choice task can often influence success rates, for instance ensuring the demonstrator, rather than the cups, is the main target of the subject's attention. In a meta-analysis of existing object-choice tasks using gaze cues (and pointing gestures), success rates were higher if the subject was kept at a distance, or restrained until the cues have been presented for a given period of time before allowing the subject to make a choice (Mulcahy & Hedge 2012). Therefore performance levels may be attributed to methodological issues involving the salience of the cue or the configuration of the sensory system (see below), rather than a species' cognitive capacity to pass the object-choice task.

The object-choice task first requires joint attention behaviour as the subject must attend to the same object as the experimenter. Looking at the same cup as the demonstrator (i.e. joint attention) may be achieved by gaze following, and then by visually fixating on the

nearest object in sight. Alternatively, looking at the same cup as the demonstrator may be achieved through shared attention, a mechanism involving awareness that one shares attention with another individual towards the same object (Baron-Cohen 1994; Emery 2000). In addition to fixating on a particular cup, subjects tested in the object-choice task must also use this information to subsequently choose a cup to obtain the hidden reward. A number of researchers have proposed that social interactions involving shared attention may also involve joint intention, a mechanism allowing others to be perceived as intentional agents, and enabling one to form a cognitive representation of one's own intention as well as another individuals' intention towards the same object or goal (Tomasello et al. 2005, Tomasello & Carpenter 2005). Together, shared attention and joint intention can enable shared intentionality in which individuals engage in collaborative interactions (Tomasello et al. 2005). Shared attention and joint intention may have evolved in humans as a means to communicate and cooperate with others through gaze following, and is thought to have influenced the evolution of human eye morphology to expose the white sclera around the iris (Kobayashi & Kohshima 1997). Having a conspicuous eye that makes gaze easier to track would benefit those engaging in shared intentionality.

Unlike other corvids, jackdaws have pale irises that may facilitate the ability to track eye/head movements. Von Bayern & Emery (2009a) have suggested that the pale iris may have evolved as a salient signal specifically to communicate within monogamous pairs where successful reproduction may be dependent on coordinating actions such as finding food, nest building and defence or feeding young. In support of this proposal, jackdaws presented with an object-choice task chose the correct food location only when paired with their mated partner, suggesting this task was performed cooperatively between pairs (von Bayern & Emery 2009b). Ravens, which have dark eyes, failed a same-species object-choice task (although it should be noted that ravens in monogamous pairs were not tested in a cooperative framework as the jackdaws were) (Schloegl et al. 2008a). It is unknown why some birds have evolved pale or brightly coloured irises, and no relationship has been found

between breeding system and iris colour in passerine birds (Craig & Hulley 2004), although this conclusion must remain tentative as the study did not control for phylogeny. There are also not enough comparative studies available to investigate whether sensitivity to gaze is more prominent in birds with brightly coloured eyes, or in monogamous species. One possibility is that jackdaws evolved pale irises independently of gaze following or breeding system. Therefore, rather than being a signal that evolved specifically between sender and receiver for the purpose of communication, the pale iris may be a cue (information can be extracted by the receiver) which could enhance gaze sensitivity between conspecifics. Alternatively, iris colour may not be related to jackdaw success in gaze following tasks. It is also unclear if the cues given by the demonstrator jackdaw in the object-choice task were from the eyes, head movement or body positioning, illustrating the lack of information in the literature regarding the cues that conspecifics may or may not be using in these tasks. In fact, we will argue that animals with laterally placed eyes will have difficulty using eye movements from conspecifics for cues in gaze following (see following section).

Ultimate factors such as predation rates, individual experience, foraging behaviours, social systems and mating systems may influence proximate mechanisms including the cognitive processes by which an animal processes information obtained from gaze cues. The dynamics of social interactions may select for the evolution of cognitive mechanisms enabling more flexible, complex forms of gaze following. Studies on conspecific gaze following in various social contexts may thus enable us to examine the interaction between sociality and cognition.

Animals' responses during experiments will also often be dependent on the specific gaze cues presented (e.g. head orientation, size, colour or shape of the eyes), as demonstrated in many gaze aversion tasks (e.g. Scaife 1976b; Jones 1980; Burger et al. 1991; Carter et al. 2008). However, gaze following tasks often assume that the cues presented to subjects reflect those the study species uses for gaze following under natural conditions, which may not be the case. Confounding factors, such as species differences in

visual configuration and hence different responses to the experimental stimuli used as gaze cues, should also be considered when interpreting results from the existing literature, and when designing gaze following experiments.

SENSORY ARCHITECTURE AND CUE INFORMATION

Consideration of sensory systems is essential to understanding instances of gaze sensitivity across taxa. For example, gaze sensitivity tasks initially designed to test underlying cognitive mechanisms in humans and other primates were designed for species with very specific visual systems: having forward-facing eyes allows gaze cues to be presented as head turning and orientating in a fixed direction, or presented as the orientation of both eyes in one direction. Whilst there is extensive work on the gaze cues used by primates (Tomasello et al. 2007), and how the eyes have evolved as a signal in humans (Kobayashi & Kohshima 1997; Kobayashi & Kohshima 2001), little is known about how other animal's visual system is configured and how they respond to different cues that could be used in gaze sensitivity contexts (e.g. eye and head movements). This is particularly important as the number of species tested in gaze sensitivity tasks broadens. Existing studies include mammals with laterally placed eyes (i.e. goats, Kaminski et al. 2005; horses, *Equus caballus*, Proops & McComb 2010), as well as reptiles (e.g. Wilkinson et al. 2010) and birds (e.g. Loretto et al. 2010; Kehmeier et al. 2011). All these species have very different visual systems. These differences are likely to influence whether test subjects can perceive the gaze cues presented in experiments. We use birds as models to discuss the influence of visual architecture on gaze sensitivity because of the relatively large comparative literature on the avian visual system. However, when possible, we discuss the visual systems of other vertebrates. Birds show a high degree of inter-specific variability in visual systems (Meyer 1977; Martin 2007) that is also present in other taxa (i.e. several species of birds, mammals and reptiles have laterally placed eyes, while others have

frontally placed eyes). Therefore, the conclusions derived from the following discussion can be applied to other vertebrate taxa subject to gaze sensitivity studies. Our main argument is that our understanding of gaze sensitivity would benefit enormously if behavioural and cognitive studies are accompanied by a detailed characterisation of the study species' visual architecture. This will determine what cues are available to indicate gaze direction and hence what cues conspecifics or heterospecifics are sensitive to.

Visual architecture

Of the many components of the visual system, the following are likely to play a particularly relevant role in gaze sensitivity: position of the orbits, visual field configuration, degree of eye movements, and type, position and number of retinal specialisations. We briefly explain each of these sensory components. Different species vary in their degree of orbit convergence (i.e. position of orbits in the skull) and thus in the extent of their binocular, lateral, and blind fields around their heads (i.e. visual field configuration) (Martin 2007; Iwaniuk et al. 2008). The placement of the orbits affects the general position of gaze in visual space as well as where other animals can detect gaze from. Bird species with more frontally placed eyes would tend to have wider binocular fields than species with more laterally placed eyes, when the eyes are at rest (Iwaniuk et al. 2008). A similar pattern has been found in mammals (Heesy 2004). However, the degree of eye movement varies substantially between species (Martin 2007; Fernández-Juricic et al. 2010), which can lead to variations in the visual field configuration. For example, some species can barely move their eyes (e.g. owls; Martin 1984), whereas others with laterally placed eyes can converge and diverge their eyes (towards and away from their bills respectively) to the point that they can have binocular fields the size of those with frontally placed eyes and extremely narrow blind areas that increase their fields of view around their heads (sparrows, Fernández-Juricic et al. 2008; Fernández-Juricic et al. 2011). Similar ranges in the degree of eye movement can be found

in other vertebrates. For instance, chameleons can move their eyes about 180º, whereas guinea pigs can only move their eyes about 2º (Ott 2001; Kim 2013). These visual field configuration changes have important functional implications for enhancing food search (i.e. widening binocular fields) and predator detection (i.e. widening lateral areas), two relevant cues in gaze following scenarios.

The position of the orbits on the head also affects where potential gaze cues are available, and therefore whether other animals can perceive eye movements. For animals with frontally placed eyes, eye movements can best be perceived from the front, where both eyes can be seen (Figure 3a). In contrast, eye movements in laterally-eyed animals can best be perceived from the side, making only one eye visible from this perspective (Figure 3a). This has important implications if an animal with laterally placed eyes is trying to detect the gaze of a conspecific who can move their eyes. If the animal is looking at the conspecific from the side, only one eye is visible. The position of the other eye is unknown to the conspecific and this can lead to ambiguity of gaze direction (Figure 3a).

Nevertheless, the size of the visual field only describes the volume of visual space animals can perceive around their heads as a result of the projection of their retinas, but not the quality of vision. Visual performance varies in different parts of the visual field because of changes in the density of photoreceptors (i.e. involved in phototransduction) and retinal ganglion cells (i.e. involved in the transfer of information from the retina to visual centres in the brain) across the retina (Hughes 1977). Areas of the retina with higher density of photoreceptors and retinal ganglion cells are known as retinal specialisations. These retinal specialisations project into a specific part of the visual field and provide higher quality information (e.g. higher visual resolution) than other parts of the retina (Collin 1999). The retinal specialisations are thought to be the centres of visual attention (Bisley 2011). In other words, when an animal detects a visual stimulus in a sector of the visual field that is outside of the retinal specialisation, it will move its head and eyes to align the retinal specialisation with that object and collect high quality information.

Retinal specialisations vary in type, size, position, and number (Meyer 1977). For instance, the fovea is a retinal specialisation characterised by an invagination of the retinal tissue whose centre provides the highest visual resolution (Walls 1942). Foveae are present in many vertebrates (Walls 1942; Duijm 1959; Hughes 1977) such as some primates and birds, but also in some canids and fish (Packer et al. 1989; Curcio et al. 1991; Peichl 1992; Collin et al. 2000; Dolan & Fernandez-Juricic 2010;). The fovea projects into a smaller portion of the visual field than the visual streak, which is another retinal specialisation that consists of an enlargement of the retinal tissue forming a horizontal band of high visual resolution across the central axis of the whole retina (Walls 1942). Different vertebrate species have been found to have visual streaks (Hughes 1977), such as horses, goats, and dogfish (Hughes & Whitteridge 1973; Bozzano 2004; Querubin et al. 2009). Additionally, the position and number of retinal specialisations can affect the direction of gaze. For instance, some Passeriformes tend to have a single fovea projecting into the lateral field (Fernández-Juricic et al. 2011), making individuals use their lateral fields (i.e. aligning their heads laterally in relation to the object of visual interest) to explore visually objects (e.g. zebra finch, *Taeniopygia guttata*; Bischof 1988). However, some diurnal raptors have two foveae, one central projecting to the lateral field and one temporal projecting into the binocular field (Fite & Rosenfield-Wessels 1975; Reymond 1985). During a chase, raptors align the fovea projecting frontally into the binocular field with the prey when close to catching it (Tucker 2000). Thus, depending on the configuration of the visual field and the retina, the behaviours associated with gaze direction would vary between species. Variations in the number and position of the retinal specialisations are also present in other vertebrates; for instance, wolves, *Canus lupus*, have a horizontal streak with a temporally placed fovea (Peichl 1992) whereas the pigtail macaque, *Macaca nemestrina*, has a single fovea (Packer et al. 1989).

Visual perception in a gaze following context

Two of the most important visual tasks for animals are visual search (i.e. looking for an object in visual space that is absent; such as searching for predators) and visual fixation (i.e. focusing gaze on an object that is present in visual space and gathering high quality visual information from it with the retinal specialisation; such as tracking a predator approaching). From the perspective of gaze sensitivity, visual fixation is a key process as it indicates the main centre of visual attention (Bisley 2011). Visual fixation is associated with specific behavioural patterns (e.g. eye and head movements); which are expected to be the cues that other animals would use during gaze detection. However, variations in the visual architecture mentioned above are likely to modify these behavioural patterns (or cues) in different ways depending on the position of the projection of the retinal specialisation in visual space. Therefore, understanding visual system configuration and fixation should be two essential elements when determining the gaze cues to which animals are sensitive.

(Please insert Figure 3 approximately here)

For example, humans have frontally placed orbits with a large degree of eye movement. In humans, the fovea is positioned at approximately the centre of the retina, hence projecting into the binocular field (Fig. 3a). When humans fixate, both foveae align with the object of interest with a steady gaze (Fig. 3b). When an object is static, human fixation is associated with a decrease in head movements and is fine-tuned with the eyes 'locked' on the target of attention (although the eyes still engage in very subtle movements; Martinez-Conde 2005). A similar visual fixation strategy is present in other vertebrates such as dogs (Somppi et al. 2012). The ocular fine-tuning in humans is facilitated by eye colouration, in which the iris surrounded by a clear sclera becomes a salient cue that facilitates gaze detection (Kobayashi & Kohshima 1997). Overall, this visual and morphological configuration in humans reduces ambiguity in gaze direction cues.

However, in many species with laterally placed-eyes (e.g. most birds, goats, horses; Fig. 3a), the type of retinal specialisation, along with its projection, varies enormously

between species. Additionally, their visual fixation strategies are not as well understood. Two visual fixation strategies have been proposed for birds with laterally placed eyes (Fig. 3b): 1) fixating only one fovea on a visual target using monocular vision (Maldonado et al. 1988), and 2) quickly alternating between the two foveae using the monocular fields of both eyes (Dawkins 2002). The first strategy is similar to human fixation in that it locks the gaze (in this case with only one eye) on the object of interest, thus reducing head movements (Fig. 3b). The second strategy actually increases head movements by having each eye check the object of interest repeatedly (Fig. 3b). Furthermore, there is evidence that fixation may also occur within the binocular field in species with laterally placed eyes when objects are very close by (Bloch et al. 1984; Dawkins 2002); however, it is not known whether this occurs by animals converging their eyes and thus projecting their retinal specialisation into the binocular field. There is a major gap in comparative data as to how fixation strategies vary in vertebrates with different visual architecture, which would influence the cues other individuals use to assess gaze direction.

We can, however, make some predictions about the combination of sensory traits that could favour (or not) gaze sensitivity in species with laterally placed eyes and a single fovea. A large number of the species belonging to the most diverse avian Order, Passeriformes, surveyed to date have a single fovea that is centro-temporally placed (Fernández-Juricic 2012), which generally projects into the lateral visual field, but not far from the edge with the binocular field. These species have, however, different degrees of eye movement. If birds use eye movement as gaze direction cues as humans do, we would expect sensitivity to gaze cues to be more prevalent in species with larger degree of eye movement (Fig. 3b), and particularly the ones in which the eye is visually salient due to a differently coloured iris (e.g. jackdaws).

Even in species with salient (i.e. brightly coloured) eyes, there is a fundamental challenge: some bird species show coordinated eye movements whereas in others the two eyes move independently of one another (Bloch et al. 1984; Voss & Bischof 2009). The

implication is that during fixation, the movement of one eye would predict the movement of the other eye in some species, but not in others (Fig. 4). This uncertainty could translate into an ambiguous gaze direction cue, which may not favour gaze detection using *only* eye movement cues (Fig. 4). Evidence in species with laterally placed eyes supports the view that birds tend to move their heads more than their eyes when changing the direction of gaze (Gioanni 1988). Consequently, we propose that in species with laterally placed eyes and a single fovea, species are more likely to be sensitive to head movement cues (e.g. head orientation, rate of change in head position, etc.) rather than eye movement cues. In those species that fixate by 'locking' their gaze to an object with a single fovea, the gaze cue is expected to be a pronounced decrease in head movement rate associated with a single head position aligned with the visual target. Conversely, in those species that fixate by using both foveae alternatively, the gaze cue would be an increase in head movement rate associated with at least two main head orientations in which each eye aligns with the visual target.

(Please insert Figure 4 approximately here)

Determining gaze cues (i.e. eye, head, body orientation postures that indicate where a conspecific is looking at) in bird species with a visual streak (e.g. anseriformes) as the retinal specialisation may be even more challenging. Most of the sensory issues described above apply, but additionally these species have a lower need to move their heads and eyes as the visual streak provides high visual resolution in a larger proportion of the visual field (the whole horizontal axis) than in species with fovea (Collin 1999). We expect that species with visual streaks may be less sensitive to gaze cues, or would rely on less ambiguous cues, such as moving the head sideways to fixate the object with the retinal specialisation of each eye alternatively; therefore, relying more on head orientation than head movement rate. Overall, we propose that visual architecture will influence not only the ability to perceive gaze cues, but also the types of cues associated with gaze direction that conspecifics and heterospecifics may use.

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COGNITION IN GAZE SENSITIVITY

A species' visual system may influence the information made available to individuals in the form of gaze cues, and socio-ecological factors may determine whether adaptive information can be gained from attending to gaze cues (e.g. the location of food). Once it has been established that gaze cues are available to the subject and that they elicit a gaze response, we can investigate the cognitive mechanisms involved in processing gaze cue information which generate behavioural outputs.

The difficulty in interpreting the cognitive mechanisms a species is applying to gaze tasks is two-fold. First, if the sensory system of an animal is not considered, it is difficult to be certain that a negative result is due to the lack of a particular cognitive mechanism as opposed to a lack of sensitivity to a particular cue. Second, if a gaze cue is available and does cause a response, it remains difficult to disentangle whether a particular action (e.g. gaze following) is driven primarily by the stimulus (e.g. eye, head movement), or if it is also driven by cognitive mechanisms that enable the subject to understand something about what the demonstrator can see. Seemingly complex behaviour may often be underpinned by relatively simple mechanisms. For example, stimulus-driven visual fixation processes in praying mantises generate complex, coordinated movements of the head, abdomen and prothorax when pinpointing the exact location of prey (Rossel et al. 1980; Yamawaki et al. 2011). Similarly, the body and eye movements apparent when vertebrates redirect their visual attention in joint attention, gaze following or geometric gaze tests may also be driven by simple stimulus-response processes. One cannot ascribe the presence of gaze sensitivity to cognitive mechanisms such as perspective taking or attention attribution (see below) simply based on the complexity of behaviours observed when animals gather visual information. Instead, carefully designed experiments are essential if we are to discriminate

between alternative cognitive explanations. Often this means that authors must present alternate interpretations in the form of ‘low-level’ (e.g. simple behavioural responses, or associative learning mechanisms) and ‘high-level’ mechanisms (e.g. perspective taking or attention attribution) because it is not always definitive which are driving the observable behaviours (e.g. Povinelli & Eddy 1996; Call et al. 1998).

Alternative interpretations

The majority of studies of the cognitive processing underlying gaze responses have employed gaze following paradigms, (but see Call et al. 2003; Flombaum & Santos 2005; von Bayern & Emery 2009a for examples of cognitive tasks applying gaze aversion paradigms). Often these studies are unable to discount alternative cognitive interpretations for observed behaviour. For instance, individuals may succeed in a gaze-following task by learning to associate finding food or an interesting object with seeing a particular gaze cue and then performing a gaze following behaviour. Alternatively, the subject may apply mechanisms such as shared attention or attention attribution. Attention attribution is similar to shared attention in that the subject appreciates where the demonstrator’s attention is focused, but does not necessarily involve attending to the same object (e.g. von Bayern & Emery 2009a).

Gaze following behaviours also raise the question of whether animals are capable of perspective taking. Perspective taking has been described as the ability to infer that others may see different things than what oneself sees (Flavell 1974; Flavell 1977). For instance, in the geometric gaze task, a subject might take into account another individual’s line of sight as being different from one’s own in order to adjust its positioning around a barrier. In the literature on non-human gaze following, mechanisms such as shared attention, attention attribution and perspective taking are typically defined as distinct from Theory of Mind (the ability to reason about other individual’s mental states, separate from one’s own). Although

Theory of Mind may guide gaze responses in humans, tasks in non-human animals cannot test for this when applying paradigms which involve behavioural cues such as eye gaze. Such tasks are unable to distinguish between responses to gaze cues themselves, as opposed to responses to another individual's mental states. The most compelling evidence for perspective taking in gaze-related tasks comes from experiments which control for gaze cues, or in fact, any behavioural cue. For example, in studies of food-caching corvids, subjects have been presented with individuals which differ only in whether they had visual access to an object (i.e. food) or an event (i.e. caching) (e.g. Emery & Clayton 2001; Dally et al. 2006; Bugnyar 2010), not in the gaze cues presented. Even so, it remains possible that demonstrators may provide subtle behavioural cues that indicate whether or not they saw food. Controlling for behavioural cues may be possible using robot models or video playback (Fernández-Juricic et al. 2006; Bird & Emery 2008; Woo & Rieucau 2012; see also below).

Interpreting negative results

If negative results are obtained in gaze tasks, we should not always presume the absence of cognitive mechanisms in the context of gaze sensitivity. Instead, failure to perform successfully in gaze tasks may occur because the appropriate gaze cues were not available to the subject. Information on sensory systems is critical to determine whether the species is capable of attending to the demonstrators' gaze cues. If it is known that a species' visual configuration presents ambiguous gaze cues or none at all, then we should rule out mechanisms such as shared attention or perspective taking, at least in the context of gaze following. Similarly, if the available gaze cues within a species have not been identified correctly, experimenters may be expecting to measure a behaviour that does not match the species' actual response-type, given their visual architecture. For example, if both gaze cues and gaze responses within a species are very subtle (e.g. small eye movements), eye movement responses may be overlooked if head movements are the expected measure.

Only once observable cues are shown to elicit measureable gaze responses can further behavioural data be collected to test for cognitive mechanisms. For example, behaviours such as turning back to face the demonstrator, presumably to confirm where they are looking (all great apes, Bräuer et al. 2005), or placing distractor objects close to the subject, but not in the demonstrator's line of sight (chimpanzees, Tomasello et al. 1999) may provide some support for shared attention. This may require the subject reliably attend to where the demonstrator is looking, rather than stopping at the first interesting object.

With all this uncertainly, which tasks are the most informative for testing underlying cognitive mechanisms? Overall, the geometric gaze task may be a good test for complex processing in a gaze-following context as it requires the subjects not only follow the gaze of others, but also act by adjusting their vantage point. This task also has the benefit of being ecologically relevant, as individuals may often encounter and move around barriers occluding their line of sight, or as we have seen, may be important in species engaging in cache protection and pilfering (e.g. Bugnyar et al. 2004; Dally et al. 2006; Schloegl et al. 2007).

APPLICATIONS FOR GAZE RESEARCH

The socio-ecological, anatomical, sensory and cognitive features we discussed may influence the occurrence of gaze behaviours across taxa, but these factors are seldom considered together when designing and interpreting gaze tasks. To address this gap and gain a better understanding of the mechanisms underlying gaze sensitivity, we propose a new approach that consists of the following steps. Following these steps could improve our ability to interpret results, particularly in studies which show null results, while also contributing to comparative data available to gaze researchers to test how the features of an animal's visual system may be associated with the gaze cues and responses.

1) Gaze researchers should study key components of the visual system of the study species (i.e. orbit orientation, visual field configuration, and type, position and number of retinal specialisations, see http://www.retinalmaps.com.au for retinal topography maps) to establish the projections of the areas of acute vision into the visual field. This may be possible by studying species that are phylogenetically closely related to the ones with existing data available, or if limited in available study species, by collaborating with researchers that study visual systems. This will aid in making predictions regarding the degree of eye and head movement expected during visual fixation, and where possible, to target species expected to display more pronounced gaze cues (e.g. head movement rates). 2) The behavioural mechanisms of visual fixation (e.g. head/eye orientation, movement rate, etc. when gaze is locked in an object) in the study species should be determined. This may involve observational data of the study species when presented with objects of interest in their line of sight, and at different distances to identify head or eye movement associated with viewing these objects (Bossema & Burgler 1980; Dawkins 2002). Observational data in this context will further our understanding of how specific features of an animal's visual architecture relate to observable gaze cues. 3) It is also important to characterise the behaviours associated with visual fixation in different contexts, for instance, are the gaze cues during food search and predator detection the same? 4) Once the gaze cues produced by the gazer are characterised, it should be established whether the cues identified in the previous step generate a gaze sensitivity response, and whether this differs depending on the social-ecological context of the task (e.g. avoiding predator gaze versus the cooperative and competitive contexts when following conspecific gaze). In order to do so in a gaze following context, it may be beneficial to use conspecifics. This is important for those testing behaviour or cognition. If a species visual fixation strategy differs from humans, the subjects may not associate human gaze in the same way they would a conspecific's gaze (but see von Bayern & Emery 2009a where subjects were hand-raised by and had extensive interactions with humans prior to testing). Therefore, failure in a task may be measuring a lack of cue perception rather than a lack of a given cognitive mechanism. We recognise that

some species are often not studied in a within-species context mostly due to logistical difficulties in manipulating gaze following cues. We suggest waiting until the appropriate gaze cue has been displayed by the demonstrator before recording subject gaze response. We also now have interesting tools at our disposal such as video playback, which has been successful for assessing same-species social preferences in rooks (Bird & Emery 2008). Gaze cues can be manipulated by using animated video playback, which has been shown to be a successful stimulus for many species of fish, some bird species (e.g. *Lonchura punctulata*, *Gallus gallus, Taeniopygia guttata*) and Jacky dragons, *Amphibolurus muricatus*, (see Woo & Rieucau 2012 for review). Cue manipulation could also be applied using robotic animals (e.g. birds, Fernández-Juricic et al. 2006). This empirical approach can be easily adjusted to test the relative role of eye vs. head movements in species with frontally and laterally placed eyes, the role of eye colour on gaze detection in birds, the relative role of different gaze following rules, etc. Alternatively, peep holes (a small hole in a wall or barrier through which the subject can look) are an effective method of determining what subjects are attending to and for how long (Bird & Emery 2010; Grodzinski et al. 2012), and could be implemented to control what cues are observable by using different sized peep holes exposing only the head or the eyes, or restricting species to use monocular vision only. Peep holes should be adjusted to the relative size of the species, as larger species (i.e. larger eye sizes) have higher visual acuity (Kiltie 2000). This could be particularly relevant in studies comparing the performance of gaze sensitivity between species (e.g. territorial vs. social).

Once gaze behaviours (i.e. gaze aversion, gaze following) have been established in response to characterised gaze cues, these can be applied to more complex tasks. For example, a task can be structured using the appropriate cue and a barrier to test geometric gaze. Although the gaze cue itself does not test cognitive mechanisms directly, understanding the gaze characteristics of the study species ensures that negative results are not due to the lack of cue perception.

CONCLUSION

In this review, we have proposed several socio-ecological, anatomical, sensory, and cognitive factors which may explain the variation in gaze following or gaze aversion responses across species. We argue that it is critical to consider an animal's visual architecture as it will directly affect their ability to detect the targets of gaze. Gaze cues can differ between contexts within the same species, for instance, whether the visual fixation strategy used by a conspecific is being presented as a cue during food search or as a cue during predator scanning. Furthermore, the gaze cues detectable between conspecifics may be different from gaze cues presented by heterospecifics or predators. Therefore it is crucial to ensure that appropriate cues are chosen to match the context of the task. This presents researchers with a unique opportunity to test how variations in sensory systems can affect the occurrence of gaze sensitivity across species. Finally, establishing the gaze cues that each species attends to, and under what conditions, will provide robust experimental designs for gaze tasks testing cognitive mechanisms.

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Figure 1. Gaze cues and behaviours. Arrows depict direction of gaze. a) direct gaze (single arrow) and mutual gaze (double arrow); b) direct gaze cue resulting in averted gaze response; c) gaze following; d) joint attention; e) geometric gaze.

Figure 2. Diagram depicting proposed gaze nomenclature. Gaze sensitivity is reliant on the gaze cues available. Sensitivity to gaze cues will result in gaze behaviours which are described within the categories of gaze preference, gaze aversion and gaze following.

Figure 3. a) In animals with frontally placed eyes, the orientation of both eyes (as cues for gaze following) is most easily seen from a frontal view, whereas in animals with laterally placed eyes, eye orientation is more salient from the side but is partial as only one eye can be seen. b) Visual fixation strategies proposed for bird species with laterally placed eyes. (I) locking the gaze on a object with a single fovea using the monocular field of one eye; (II) quickly alternating between the two foveae using the monocular fields of both eyes (see text for details).

Figure 4. Gaze direction cues may have different degree of ambiguousness in animals with laterally placed depending on whether a species has conjugate or non-conjugate eye movements. (I) Conjugate eye movements with eyes converging towards the bill. (II) Conjugate eye movements with both eyes looking to the right. (III) non-conjugate eye movements where the left eye looks forward and the left eye is at rest towards the left side.

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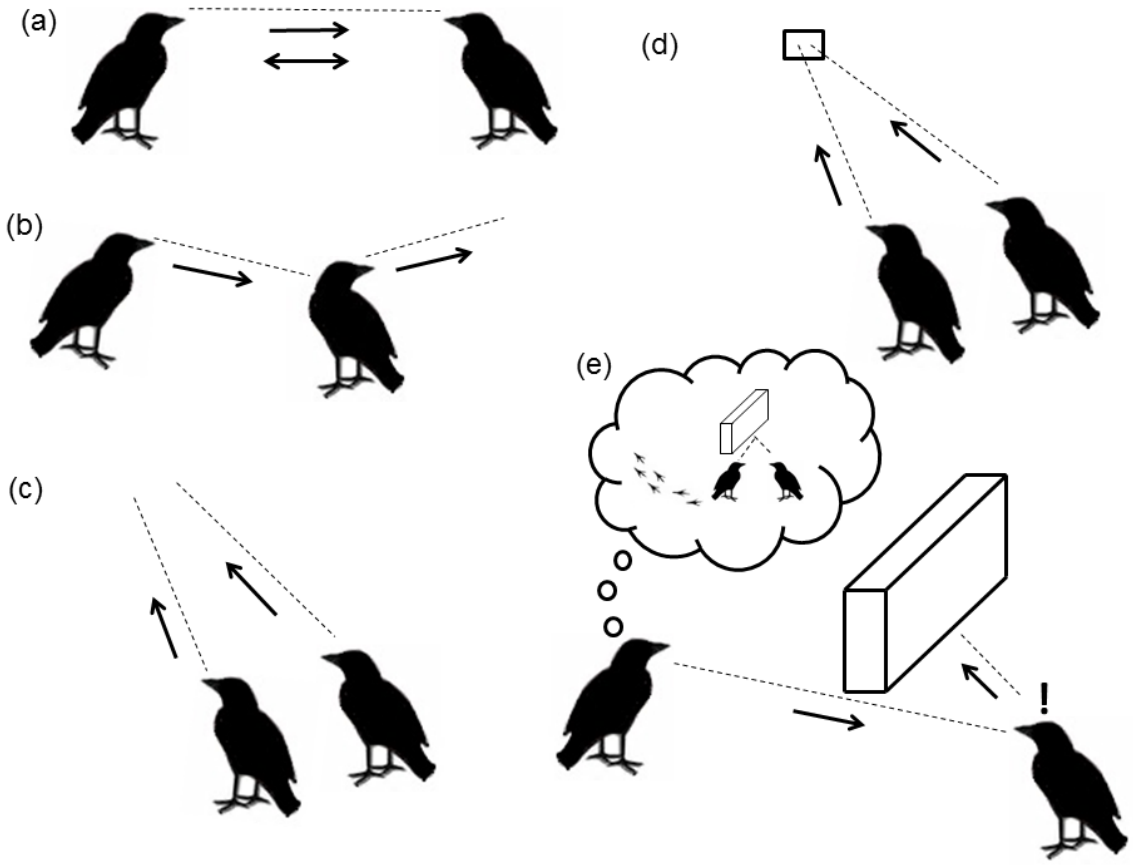
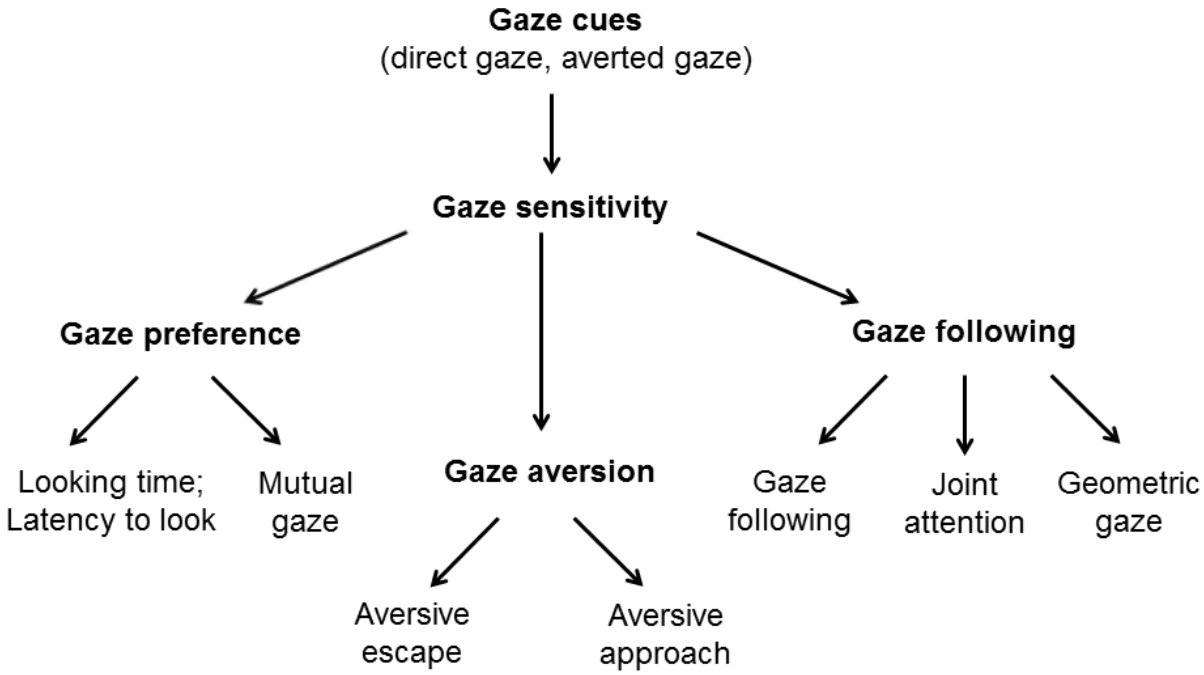
Figure 1



1102 Figure 2



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1104 Figure 3

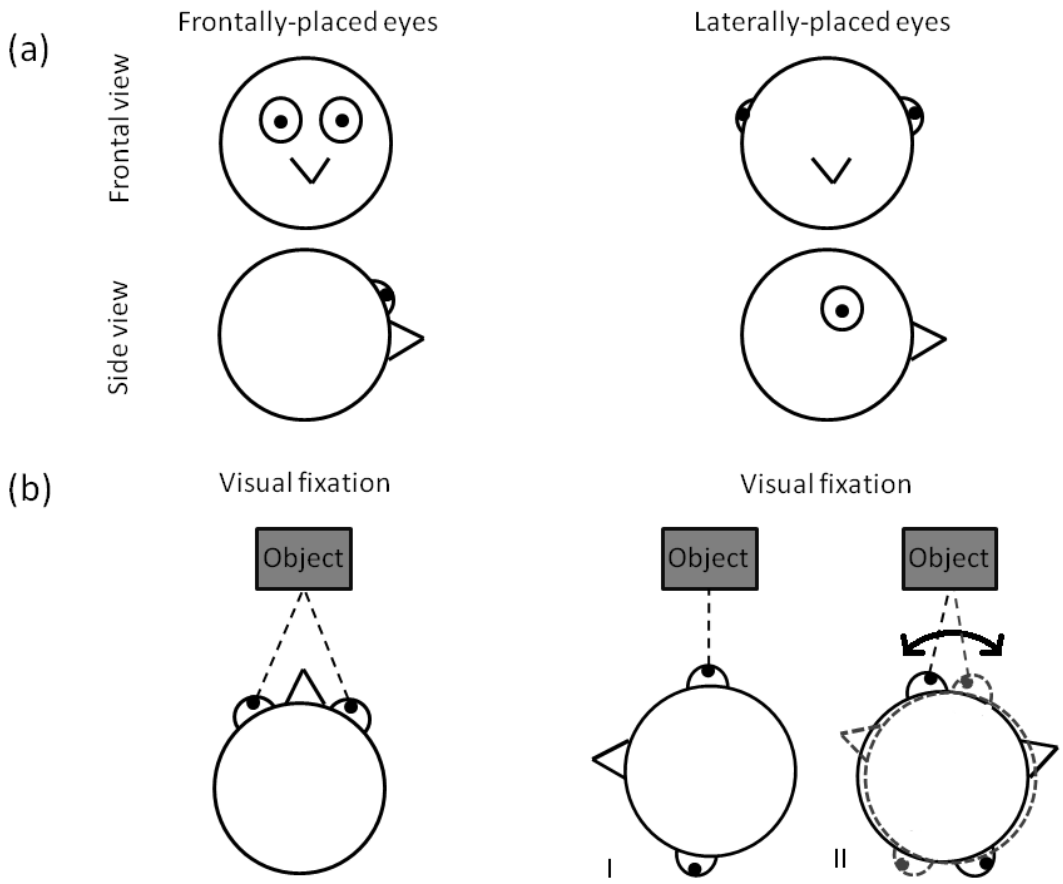

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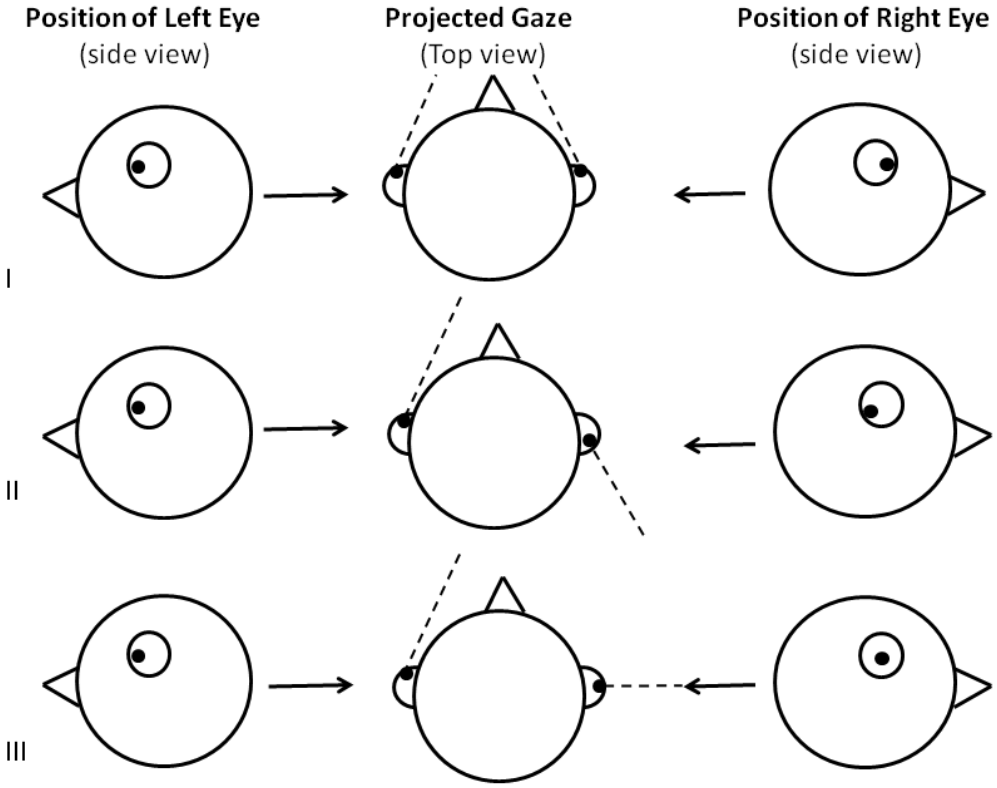
Figure 4


Position of Left Eye
(side view)
Projected Gaze
(Top view)
Position of Right Eye
(side view)
I
II
III