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Review

Gaze sensitivity: function and mechanisms from sensory and cognitive perspectives

Gabrielle L. Davidson [a,*], Shannon Butler [b], Esteban Fernández-Juricic [b], Alex Thornton [a,c], Nicola S. Clayton [a]

[a] Department of Psychology, University of Cambridge, Cambridge, U.K.
[b] Department of Biological Sciences, Purdue University, West Lafayette, IN, U.S.A.
[c] Centre for Ecology and Conservation—Biosciences, University of Exeter, Penryn, U.K.

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Sensitivity to the gaze of other individuals has long been a primary focus in sociocognitive 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 socioecology, sensory systems and possibly also their underlying cognitive mechanisms. Furthermore, as more species are found to exhibit gaze sensitivity, more terminology arises to describe the behaviours. 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 nonhuman animal studies where cognitive interpretations are ambiguous. We then describe how socioecological 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 specializations 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 socioecology and visual systems to advance the field of gaze research.

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 show gaze sensitivity in many contexts: we can accurately follow where others are looking in space (e.g. Bock, Dicke, & Their, 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, Alexis, Clayton, & Davis, 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-orienting with another's gaze to spot objects of interest. Behavioural and sensory ecologists have sought to determine the socioecological contexts in which gaze sensitivity occurs, and to identify features of cues that are most important for eliciting gaze sensitivity responses (e.g. Burger, Gochfeld, & Murray, 1991; Carter, Lyons, Cole, & Goldsmith, 2008; Hampton, 1994; Watve et al., 2002). 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. von Bayern & Emery, 2009a; Bugnyar, Stowe, & Heinrich, 2004; Loretto, Schloegl, & Bugnyar, 2010). The study of this information processing has been of great interest to cognitive psychologists (e.g. Call, Hare, & Tomasello, 1998; Povinelli & Eddy, 1996). 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 standardized set of nomenclature that brings together all aspects of

* Correspondence: G. Davidson, Department of Psychology, University of Cambridge, Downing Street, Cambridge CB2 3EB, U.K.
E-mail address: gd339@cam.ac.uk (G. L. Davidson).

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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 socioecological 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 orient 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 orient 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 nonhuman 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 that 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 in which multiple disciplines study gaze sensitivity. For those studying underlying cognition, experimental paradigms can be applied specifically to 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 prerequisite 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

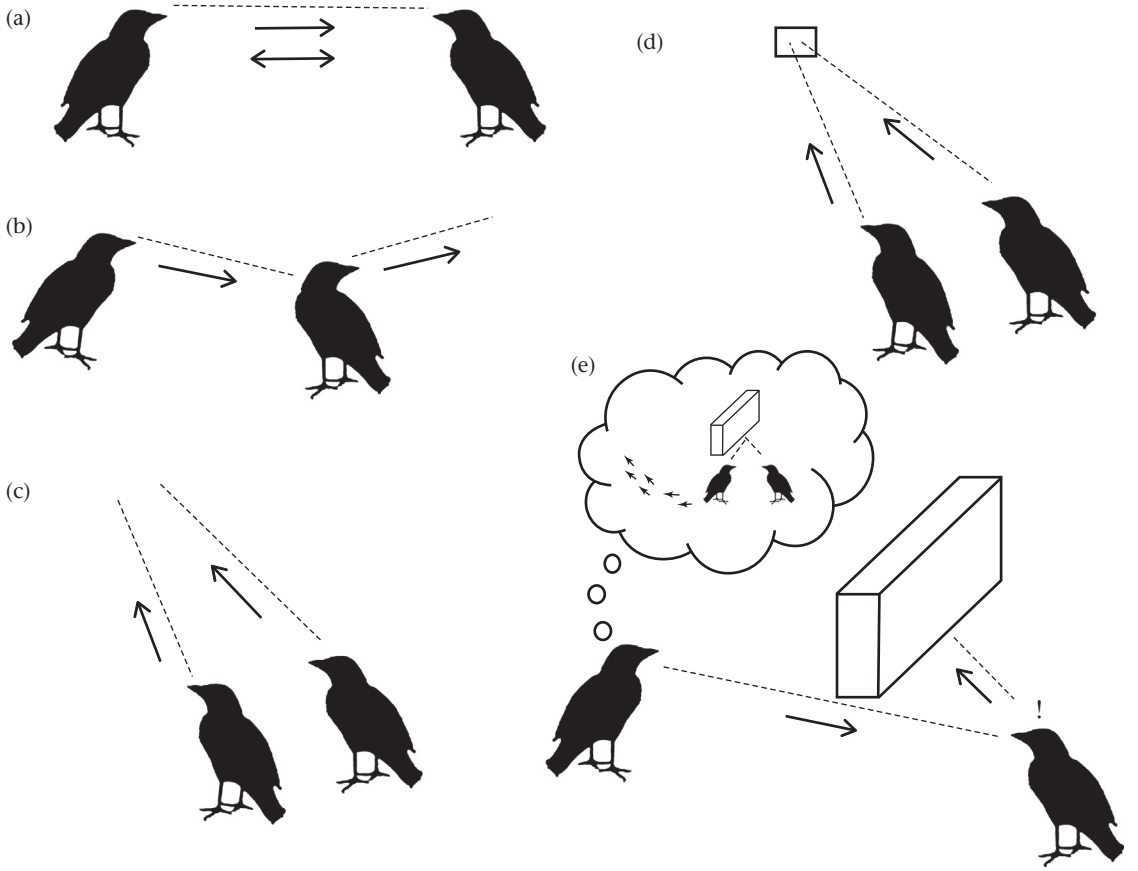

Figure 1. Gaze cues and behaviours. Arrows depict direction of gaze. (a) Direct gaze (single arrow) and mutual gaze (double arrow); (b) direct gaze cue resulting in averted gaze response; (c) gaze following; (d) joint attention; (e) geometric gaze.