



PERSPECTIVES AND REVIEWS

Perspectives: The Looking Time Experimental Paradigm in Studies of Animal Visual Perception and Cognition

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Abstract

Experiments are the foundation of empirical science, and experimental paradigms that are broadly applicable across settings and species are particularly useful for comparative research. Originally developed to address questions related to perception and cognition of pre-verbal human infants, the looking time experimental paradigm has been increasingly used to study animal behavior and cognition, particularly in non-human primates. Looking time experiments are based on the assumption that animals direct eye gaze toward objects or scenes based on their degree of interest, and use looking behavior to infer perceptual or cognitive characteristics of subjects. This paradigm can be used in a variety of contexts and is not based on species-typical behaviors, allowing for intra- and interspecific comparisons. Here, we describe the history of use of looking time measures, provide an overview of the problems and controversies related to this method, and offer recommendations on how to implement looking time tasks, focusing on the preparation of stimuli, experimental procedures, and data analysis. Our overview focuses on non-human primates, where most work has been carried out, but the issues discussed should be applicable to a wide range of species. We conclude that despite pertinent criticism, looking time tasks are practical when executed and interpreted properly. The further implementation of these methods in studies of animal behavior and cognition is likely to be fruitful.

Introduction

While much scientific insight can be gained from correlational studies, experiments allow for increased control of potentially confounding variables and provide greater confidence in causal relationships. One experimental paradigm that has increasingly been used in the animal cognition and behavior literature is the looking time paradigm. Originally developed for research involving pre-verbal human infants (Berlyne 1958; Fantz 1958), looking time tasks involve the presentation of visual stimuli and the measurement of subjects' corresponding eye gaze toward each stimulus. Interpretations of the subjects' perceptive or cognitive abilities are then made based on the patterns of eye gaze observed (Spelke 1985). As such looking time tasks can be conducted in any species in which the direction of eye gaze can be measured and can be

implemented in various settings, this allows for intra- and interspecific comparison in behavior, perception, and cognitive abilities. Despite the increased use of this paradigm in studies of non-human animal (hereafter 'animal') cognition and communication, to our knowledge, there has been no systematic review of the methodologies, assumptions, and the analytical issues that pertain to its use on animals. Here, we discuss the history and philosophy of the looking time experimental paradigm, provide examples of its implementation, and assess the utility of these methods for studying perception and cognition. We emphasize non-human primates (hereafter, 'primates') due to research biases toward this group, but our discussions are pertinent to a wide range of taxa and we hope that this review will inspire further research in non-primate groups. We propose guidelines on how to conduct looking time experiments,

particularly in free-ranging settings. Note that multiple terms have been used in the literature to describe research of the sort we discuss here; these terms include (but are not limited to) looking time, eye gaze, visual fixation, orientation, attention, preferential looking, and (particularly in non-human research) visual paired comparison. Throughout this review, we use the term 'looking time' to denote the duration of eye gaze toward a particular target, although it could potentially be replaced by some of these other terms.

The History and Implementation of Looking Time Paradigms

The birth of looking time paradigms is generally traced to Robert Fantz's research on perception in human infants in the late 1950s and early 1960s (e.g., Fantz 1958, 1961, 1963, 1964; Fantz & Ordy 1959; Fantz et al. 1962). While some previous studies had used measurements of looking behavior to assess the perceptual abilities of human infants (e.g., Valentine 1914; Staples 1932; Berlyne 1958), it was Fantz's work that ushered in an era of looking time research in the field of developmental psychology. Since its conception, the looking time experimental paradigm has spawned a wide variety of research into the perceptual and cognitive abilities of humans and other animals, and the development of multiple offshoots of Fantz's original procedure have allowed for further elaboration of the paradigm.

Looking Time Methods

All looking time tasks stem from a common assumption, namely that subjects look longer at objects or scenes that are, for one reason or another, more interesting to them. The characteristics driving increased interest may vary, including, for example, attractiveness, novelty, familiarity, and violation-of-expectations. In the absence of corroborating data, increased looking time should generally be interpreted simply as discrimination between stimuli, not necessarily as an overall preference *per se*. Therefore, we use the phrase 'visual bias' here to refer to the visual stimuli that received more attention in looking time tasks and avoid the commonly used expression 'preference'.

Multiple experimental methods have been developed to assess the presentation of visual stimuli; these include (1) visual bias tasks, (2) habituation tasks, and (3) violation-of-expectation tasks. Visual bias tasks, often referred to as 'visual preference tasks' in the literature, are those originally developed by Fantz and

are theoretically the most straightforward. In these tasks, multiple visual stimuli are presented either simultaneously or sequentially, and subject visual biases are assessed based on the looking time elicited by each stimulus. For example, in his initial study, Fantz (1958) simultaneously presented infants with various patterns and found that they looked longer at (i.e., they displayed a visual bias for) more complex patterns compared to simpler ones.

In visual habituation tasks, subjects are repeatedly presented with a stimulus until they consistently show a reduced response (i.e., they have habituated to its presentation; Jeffrey & Cohen 1971; Colombo & Mitchell 2009). In the commonly used habituation–dishabituation task, after a specified habituation criterion has been achieved subjects are then presented with a new stimulus and their reaction is recorded, with an increase in looking time ('dishabituation') compared to the habituated response indicating a detection of the difference between stimuli. Other methods are also used, including the analysis of differences in habituation time across subjects and stimuli. Habituation tasks can be very useful, for example in studies attempting to identify a threshold of discrimination between stimuli; however, they are used less frequently than other looking time tasks because the habituation process can be experimentally time consuming.

Finally, in violation-of-expectation tasks, subjects are presented with visual scenes that either do or do not conform to the subjects' hypothesized expectations about the physical or social world. A difference in looking time between trials, usually with longer looking time toward stimuli that violate hypothesized expectations, is interpreted as recognition of this violation. These variations on the looking time paradigm have been used to study the perception and cognition of human infants as well as other animals.

Looking behavior has been measured in a variety of ways. Early experiments in human infants relied on experimenters' observations of looking behavior during the trial (e.g., using a timer to calculate looking duration, Fantz 1963). Later research primarily involved video recording of trials followed by subsequent coding of videos to determine looking behavior (e.g., Bogartz et al. 1997; Waitt et al. 2003; Dubuc et al. 2009; Hughes et al. 2014), improving the precision of measurements and also allowing for assessments of inter-rater reliability. More recently, eye tracking technology has been used to assess looking behavior in both humans (reviewed by Gredeback et al. 2009; Mele & Federici 2012) and other animals (see below). Eye tracking technology is advantageous

because it allows for automated coding and under ideal conditions can provide very detailed information about the precise direction of eye gaze.

Eye tracking is generally accomplished in one of two ways: using head-mounted hardware or via external hardware. Both techniques rely on optical eye tracking, or video oculography, in which light reflected from the eyeball is measured to determine the direction of eye gaze. There are multiple methods of accomplishing this (reviewed by Hansen & Ji 2010), but most current eye trackers make use of corneal reflections of infrared light projected by the eye detector. Head-mounted systems are advantageous in that they can track eye gaze patterns in moving subjects, but they also require that hardware be physically attached to subjects, which is not always feasible. Head-mounted eye tracking systems have been developed for a variety of species, including chickens (Schwartz et al. 2013), peahens (Yorzinski et al. 2013), starlings (Tyrrell et al. 2014), rats (Wallace et al. 2013), dogs (Williams et al. 2011), and chimpanzees (Kano & Tomonaga 2013). Externally mounted devices allow eye gaze to be tracked without handling subjects, but require that subjects remain relatively stationary throughout trials and generally involve a calibration session to set subject specific eye parameters before each trial. This approach has been used especially in dogs (e.g., Williams et al. 2011; Somppi et al. 2012; Téglás et al. 2012) and primates (e.g., Dahl et al. 2007, 2009, 2010, 2013; Kano & Tomonaga 2009, 2010; Hirata et al. 2010; Kano et al. 2011; Leonard et al. 2012; Myowa-Yamakoshi et al. 2012; Paukner et al. 2013; Méary et al. 2014). Due to methodological and technological constraints, eye tracking can be difficult to implement in non-humans and, to our knowledge, has thus far only been used in controlled captive conditions. Nonetheless, studies using eye tracking methods have yielded a number of new insights, and advances in technology make the wider use of this approach more feasible.

Human Infant Research

Looking time methods have been used for over 50 yrs to study perception and cognition in pre-verbal human infants. Early research concentrated on documenting the visual perceptual abilities of infants, such as those related to color, form, and pattern. These initial studies primarily used visual bias tasks to determine whether infants could differentiate between stimuli (e.g., colors, for a review see Teller & Bornstein 1987), or exhibit a visual bias toward some stimuli over others (e.g., patterns of greater complexity,

Fantz 1958). Focus gradually shifted from these perception-oriented tasks toward the study of infant cognitive abilities. Numerous studies have used looking time tasks to assess human infants' responses to objects (e.g., object permanence, unity, and individuation) and faces, and to assess their capacity for understanding categories, numeration, and causality (for reviews of infant cognition research, see Spelke 1985; Cohen & Cashon 2003). Violation-of-expectation tasks are particularly common in this type of research, with most studies comparing looking time in trials in which potential expectations (e.g., about physical principles) are violated compared with those in which they are not. While the use of looking time in this context has not been without critique, it is nonetheless used extensively throughout the human infant literature and has been central to efforts aimed at understanding human infant perceptive and cognitive abilities.

Primate Research

Looking time-based research in animals has followed a similar trajectory to that involving human infants, with initial research focusing primarily on documenting perceptual abilities and more recent research generally focusing on cognitive processes. The first research using looking time measures in non-humans focused on perceptual abilities of captive primates, with particular emphasis on their reactions to photographs. These experiments showed that, in a variety of primate species, naïve individuals can recognize objects in photographs, particularly when they are biologically relevant items such as food or conspecifics (reviewed by Bovet & Vauclair 2000). Primates do respond to the information content of images (Humphrey 1972), but a general lack of behavioral response to photographs compared to the actual stimuli they depict suggests that they do not equate photographs with the objects or individuals they represent. For instance, primate subjects show a lack of reaching behavior toward photographs of food objects (Bovet & Vauclair 1998) and only rarely respond to photographs of conspecifics behaviorally (Humphrey 1972; Demaria & Thierry 1988; Waitt et al. 2003). However, when behavioral responses do occur, they are generally contextually appropriate (Waitt et al. 2003, pers. obs.).

Following the gradual shift toward a focus on cognition, looking time experiments on captive primates have been used to study how primates understand objects and social situations. For example, primates can classify objects (Kyes et al. 1992; Bovet & Vauclair

1998), match objects across sensory modalities (Dav-enport et al. 1975; Malone et al. 1980; Tolan et al. 1981), enumerate objects (Uller et al. 2001), and process images and videos of objects (Kano & Tomonaga 2009, 2011; Kano et al. 2011). They can also recognize themselves in videos (Anderson et al. 2009), differentiate between species (Fujita 1987; Demaria & Thierry 1988; Dufour et al. 2006; Méary et al. 2014), recognize individuals (Rosenfeld & Van Hoesen 1979; Dasser 1987, 1988; Kyes & Candland 1987; Bovet & Deputte 2009; Hanazuka et al. 2013), link visual attention to actions (Santos & Hauser 1999), recognize familiar goal-directed behavior (Rochat et al. 2008; Myowa-Yamakoshi et al. 2012), and understand features of tools (Santos et al. 2003). Recent studies have also shown that attention to images can be influenced by emotional state (Bethell et al. 2012) and by the ovulatory phase of female subjects (Lacreuse et al. 2007). A variety of primate species have demonstrated a novelty bias for objects (Pascalis & Bachevalier 1998) and conspecific faces (Pascalis & Bachevalier 1998; Gothard et al. 2004, 2009), but some also show a bias for (familiar) conspecific compared to (novel) heterospecific faces (Fujita 1987; Demaria & Thierry 1988; but see Méary et al. 2014). Research employing looking time methods has also been used to assess how primates process images of faces (reviewed by Parr 2011). Such studies may have diverse but related aims, such as identifying face regions that attract the most eye gaze (e.g., Hirata et al. 2010; Leonard et al. 2012), assessing inversion effects (Dahl et al. 2010, 2011; Hirata et al. 2010) and facial configurations (Paukner et al. 2013), comparing face processing across species (Dahl et al. 2007, 2009; Neiworth et al. 2007; Hattori et al. 2010; Kano & Tomonaga 2010), and tracking the ontogeny of face processing (Myowa-Yamakoshi & Tomonaga 2001; Myowa-Yamakoshi et al. 2005; Dahl et al. 2011, 2013). Primates also discriminate corresponding visual and auditory stimuli from mismatched/disconnected ones (Ghazanfar & Logothetis 2003; Evans et al. 2005; Bovet & Deputte 2009; Silwa et al. 2011). Looking time experiments have been used to assess the perception of visual signals in captive primates, including investigations of the salient features of eyes in lesser mouse lemurs (Coss 1978), sexual dichromatism in *Eulemur* species (Cooper & Hosey 2003), and sexual skin coloration in male and female rhesus macaques (Waite et al. 2003, 2006; Gerald et al. 2007) and male Japanese macaques (Pflüger et al. 2014). Finally, looking time methods have been used in clinical neuroscience research to study the effects of factors such as brain lesions (Bachevalier et al.

1993; Nemanic et al. 2004; Pascalis et al. 2009; Zeamer et al. 2010, 2014; Zeamer & Bachevalier 2013) and alcoholism (Golub et al. 2014).

Armed with the knowledge acquired via studies of human infants and captive primates, primatologists have more recently begun to use looking time tasks to study primates in the field. Unlike some techniques used to study captive primates that require complicated testing procedures and/or extensive training, looking time tasks can be used in both captive and free-ranging populations with no training required. This permits experiments to be conducted under more naturalistic conditions, while still allowing direct comparisons with populations held in captive conditions (Hauser & Carey 1998). The use of such methods in free-ranging primate populations has been initiated in the rhesus macaque (*Macaca mulatta*) population on Cayo Santiago (Fig. 1), a small island off the East coast of Puerto Rico (for details on the population, see Rawlins & Kessler 1986). The majority of studies using looking time tasks at this site have focused on aspects of primate cognition such as numerical representations (Hauser et al. 1996), object visual representations (Munakata et al. 2001; Shutts et al. 2009), object individuation (Uller et al. 1997; Cheries et al. 2006), object rotation (Hughes & Santos 2012), an understanding of solidity (Santos & Hauser 2002), and the representation of knowledge states (but not beliefs; Marticorena et al. 2011). More recently, research has moved more into the domains of social behavior and communication. Studies in these areas include investigations of sexual signaling (Higham et al. 2011; Hughes et al. 2014; Dubuc et al. in review), attentional biases to threat (Mandalaywala et al. 2014), and paternal kin recognition (Pfefferle et al. 2014). Such methods have also been applied to other free-ranging macaque populations. For exam-



Fig. 1. A rhesus macaque participating in a looking time task on Cayo Santiago.

ple, Schell et al. (2011) used looking time methods to study how the recognition of other group members develops in free-ranging Barbary macaques at Rocamadour visitor park in France.

Non-Primate Animal Research

Looking time tasks can be conducted in any species in which the direction of eye gaze can be measured; while most looking time research has been conducted in primates, this approach has recently also been applied to other animal taxa. The cognitive and social behavior of domestic dogs (*Canis familiaris*) has seen increased research focus recently, and looking time studies have shown that dogs understand numerosity (West & Young 2002), understand physical properties of occluded objects (Pattison et al. 2010), exhibit sex differences in object permanence (Müller et al. 2011), recognize the content of 2D images (Somppi et al. 2012), recognize conspecific and human faces (Racca et al. 2010), direct preferential attention toward their owner (Mongillo et al. 2010), recognize the correspondence between their owner's face and voice (Adachi et al. 2007), differentially respond to communicative behaviors (Téglás et al. 2012), discriminate between human facial expressions (Nagasawa et al. 2011), look longer at familiar conspecific and human faces (Somppi et al. 2014), and preferentially attend to eyes in conspecific and human faces (although to a lesser degree in inverted faces; Somppi et al. 2014).

The looking time paradigm has also been used in other groups. For instance, it has been used to show that dolphins can recognize conspecific and human faces (bottlenose dolphins, *Tursiops truncatus*: Thielges et al. 2011), and exhibit visual laterality with respect to object familiarity (captive bottlenose dolphins, *T. truncatus*: Blois-Heulin et al. 2012; wild striped dolphins, *Stenella coeruleoalba*: Siniscalchi et al. 2012). It has also been used to show that birds can express social preferences (rooks, *Corvus frugilegus*: Bird & Emery 2008), look longer at biological relevant stimuli than basic stimuli (European starlings, *Sturnus vulgaris*: Tyrrell et al. 2014), and selectively attend to certain components of visual signals (peahens, *Pavo cristatus*: Yorzinski et al. 2013). The recent application of eye tracking methods in a number of species (chickens: Schwartz et al. 2013; peahens: Yorzinski et al. 2013; starlings: Tyrrell et al. 2014; rats: Wallace et al. 2013) is encouraging and provides a promising avenue for future research.

Based on the successful implementation of the looking time paradigm in these taxonomically diverse groups, there is good reason to believe that this work

could be further expanded and applied to other taxa and to naturalistic and even wild animal populations.

Problems and Controversies

While the looking time paradigm has been widely used, it remains a controversial methodology. This is especially true in human infant research, which is perhaps surprising given the method's central position in this field. Most critiques of looking time tasks are centered around (1) the interpretation of increased looking time, (2) the differences between results based on looking time and those based on other behavioral indicators, and (3) the inclusion of proper controls.

Looking time tasks use measures of eye gaze as the response variable; however, it is not always clear precisely what an observed change in looking time actually means. Visual biases are not always consistent and are subject to change based on characteristics of the stimuli in question. For example, it is commonly assumed that subjects will look longer at novel compared to familiar stimuli. Although visual biases for novel stimuli are common in both human infants and primates (e.g., Fantz 1964; Quinn & Eimas 1996; Pascalis & Bachevalier 1998; Gothard et al. 2004, 2009), in some circumstances, subjects have also exhibited biases for familiar stimuli (e.g., Fujita 1987; Demaria & Thierry 1988; Roder et al. 2000; Shinskey & Munakata 2005), and it is not always clear *a priori* whether a visual bias for novelty or familiarity may be predicted in a given task. Preferences for familiar or novel stimuli can also be influenced by factors such as the degree of familiarity (Richmond et al. 2007) or the type of stimuli (Park et al. 2010). Given that increased looking time can be driven by multiple factors that are sometimes unpredictable, the safest interpretation of a difference in looking time between trials is that the subjects can discriminate between stimuli. When a research question requires the demonstration of an actual preference, it may be necessary to conduct additional experiments or corroborate looking time measures by comparison with other behavioral indicators.

A second critique of the looking time paradigm is that there are occasional discrepancies between results based on looking time and those based on other behavioral indicators. In human infants, different conclusions have been reached depending on whether tasks have been based on looking time or on other measures, such as reaching tasks, searching tasks, or verbal responses (e.g., Hofstadter & Reznick 1996; Ahmed & Ruffman 1998; Shinskey & Munakata

2005; Charles & Rivera 2009). The same problems have been reported for human children (e.g., Garnham & Ruffman 2001; Hood et al. 2003; Langer et al. 2003) and primates (Santos & Hauser 2002; Santos et al. 2006). This shows that it is not always clear whether and how a visual bias translates to a behavioral response. These discrepancies cast doubt on the use of looking time as the sole method for understanding a subjects' cognitive state and demonstrate the need for other corroborative measures (Kagan 2008).

Finally, many critiques of looking time studies focus on a frequent lack of experimental controls. Some classic looking time studies have failed to replicate when attempted by other researchers (see replications in Bogartz et al. 1997; Rivera et al. 1999; Wakely et al. 2000), suggesting that uncontrolled confounding variables may have been responsible for the results of the original study. Accordingly, the conclusions of some studies have been revised following the addition of appropriate controls. These include controls for the physical properties of displays (e.g., Haith 1998; Thelen et al. 2001), relative familiarity vs. novelty of stimuli (e.g., Rivera et al. 1999), and sequences of stimuli presentation (e.g., Bogartz et al. 1997). These results highlight the importance of careful experimental design and execution.

Many of the criticisms of looking time research have arisen because of poorly controlled experiments or overinterpretations of results. Therefore, despite these criticisms, the looking time experimental paradigm is still a valid methodology that can yield interesting results when implemented and interpreted properly. To produce valid results, experiments should be designed to control as many factors as possible, and differences in looking time should be interpreted conservatively as the ability to distinguish between stimuli rather than as overall preferences (at least in the absence of other corroborating data). Given the issues raised here, it is apparent that much care should be taken to design the methods and stimuli used in a looking time task carefully. In the following section, we discuss a number of relevant methodological considerations.

Methodological Considerations

Stimuli Selection and Preparation

The presentation of visual stimuli is critical to the looking time paradigm. Types of visual stimuli include, but are not limited to, photographs, videos, models, and live-action performances. In most experiments, pairs

or classes of stimuli are designed to differ in one feature of interest, thus allowing resulting differences in looking time (or lack thereof) to be interpreted as a response to differences in this feature. As in all experimental methodologies, it is therefore important in looking time based tasks to standardize all aspects of the visual scene aside from the feature of interest as much as possible. In presenting faces of conspecifics, for example, the direction of eye gaze and head orientation of the stimulus face may influence subject looking behavior (Sato & Nakamura 2001; Leonard et al. 2012). In primates, a direct gaze could be interpreted as a threat by the subject tested, and images of faces gazing directly at the camera should be avoided in stimuli (e.g., Waitt et al. 2003). Similarly, when different individuals are represented, they should be matched as closely as possible for any social, morphological, or physiological characteristics that are not under study but may vary systematically with the variable of interest. Where possible, stimuli should be approximately life-sized and should include a standardized yet naturalistic background (Fleishman & Ender 2000). Images can either be presented naturally (e.g., Higham et al. 2011), as composites (e.g., Waitt et al. 2003, 2006; Gerald et al. 2007), or after having been otherwise digitally manipulated (e.g., Cooper & Hosey 2003), but different images should all contain similar degrees of manipulation. Multiple stimuli should be used wherever possible as the stimuli are actually the unit of analysis (i.e., considering the reactions of multiple subjects to a single stimulus independently would constitute pseudoreplication). As several subjects should ideally be tested with each stimulus, the number of subjects available may set an upper limit on the number of stimuli used.

When preparing stimuli, it is essential to consider the sensory systems of the intended receiver(s). Human vision differs to various degrees from that of other animals (Jacobs 1981, 1993; Waitt & Buchanan-Smith 2006; Erichsen & Woodhouse 2012), such that stimuli differences that are perceptible to humans may not be apparent to other animal species, and vice versa. For example, the orange pelage colors of many New World primates appear conspicuous to humans, but would be cryptic against a green foliage background to dichromatic conspecifics (Sumner & Mollon 2003). Characteristics of animal visual systems that are highly variable between and even within taxa include color and luminance perception, motion detection, depth perception, and visual acuity.

Color perception varies across species and is influenced primarily by the types of photoreceptors in the

eye, their peak spectral sensitivities (i.e., the wavelengths at which they are maximally stimulated), and the relative proportions of these receptors. If color (the relative absorption and reflectance of different wavelengths of light) and/or luminance (the relative lightness to darkness of that function) need to be produced accurately in stimuli, then a number of factors involving both stimuli creation and display need to be considered. Where possible, it is best to create stimuli based on models of animal vision that use species-specific sensory information to estimate the way a species sees colors (Endler & Mielke 2005; Stoddard & Prum 2008), which is likely to lead to more biologically meaningful results (Stevens et al. 2009; Higham et al. 2010). Depending on the question under study, differences in signal content should be either detectable or indiscriminable to receivers, with one possible way of quantifying this based on units of 'just noticeable differences', which specify differences in color or luminance in units of a species' perception (Stern & Johnson 2010).

It is important to measure the colors of stimuli such as photographs and models to confirm that they conform to expectations. Printers often produce differing results both between and within machines across time (Stevens & Cuthill 2005). Techniques can be used that produce images that are indiscriminable from the original stimuli, such as an iterative printing process that involves sequential printing, testing, and refinement (e.g., Higham et al. 2011). An alternative is to undertake a printer calibration (e.g., using hardware and software combinations such as the ColorMunki© suite; Dubuc et al. in review), although it remains necessary to test the final results before stimuli are used. Similarly, most electronic devices are tuned to human vision, which may not be appropriate for other species (Cuthill et al. 2000; Fleishman & Endler 2000), and electronic displays must therefore be calibrated based on the target species' visual system (Emmel & Hersch 2000). Even when variation in color between stimuli is not part of the experimental design, it may be beneficial to verify that the colors exhibited resemble the original stimuli to minimize confounds.

Many species also exhibit differences in motion detection, which is of principal concern when using video as a stimulus. Video consists of many images shown in quick succession; when the frame rate is above a certain threshold, known as the critical flicker–fusion frequency, the presentation of still images is perceived as fluid motion by the visual system. However, the critical flicker–fusion frequency differs across species, and if the frame rate of the video

is lower than the critical flicker–fusion frequency of the target species, then the video will be seen to flicker rather than display fluid motion (D'Eath 1998). This is obviously problematic when attempting to portray a moving image. Care must therefore be taken to ensure that video images are perceived as expected in the target species, and in some cases, tuning of video parameters such as frame rate may be necessary.

Considering depth perception is also important. When conveying a three-dimensional scene in two dimensions, such as via a photograph or video, there is an inherent loss of depth information. Some depth cues are more likely to be preserved than others, which may lead to differential loss of depth information across species (D'Eath 1998; Zeil 2000). The loss of depth cues can prevent the proper representation of texture and can create spatial aliasing and other image artifacts (Fleishman & Endler 2000). Further, the angle and distance from which a stimulus is viewed may alter the extent to which information about depth is available (D'Eath 1998). Oliveira et al. (2000) suggest following two rules that can help mitigate the effects of attempting to convey depth in video: (1) animals in the video should be life size and (2) textured backgrounds should be avoided. While this may work in some circumstances, ultimately there is no way to convey depth in two dimensions properly; if accurate portrayal of depth information is needed, either because it is a focus of the study or because it is necessary for object recognition, it may be better to use three-dimensional displays such as models or live-action presentations.

Finally, it is essential to consider visual acuity. Both the distance to the stimulus and the resolution of the stimulus should be altered such that the target species can perceive the requisite level of detail, with the stimulus appearing neither blurry nor pixelated. A good rule of thumb is to ensure that the angular separation of the pixels in the stimulus is always considerably smaller than the minimum separable angle of the target species' visual system (Fleishman & Endler 2000). Similarly, in some circumstances, characteristics of the visual system or the display may cause subjects to perceive colors differently. In many types of stimuli (e.g., photographs, videos), all colors are represented using red, green, and blue pixels; adjacent pixels are blended by the visual system, so different colors can be simulated by adjusting the intensity of pixels of these three colors. Species with high-visual acuity or those that are very close to a display may actually perceive these pixels individually without blending, so that they would perceive a series of col-

ored dots rather than seeing the image as intended (D'Eath 1998; Fleishman & Endler 2000).

For those species in which the visual system has not been well-characterized, pilot studies may be needed to verify that stimuli are perceived as predicted with respect to color, motion, depth, and resolution. In many cases, looking time experiments themselves can be used to do this. Different target species may also present additional issues, such as polarized light detection (Fleishman & Endler 2000), which is why it is important to consider every relevant aspect of the target species' visual system when creating stimuli. For more information, interested readers can consult publications assessing methods related to the use of photographs (Stevens et al. 2007; Bergman & Beehner 2008), video (D'Eath 1998; Fleishman et al. 1998; Fleishman & Endler 2000; Oliveira et al. 2000), computer-manipulated stimuli (Baldauf et al. 2008), and computer animations (Woo & Rieucau 2011).

Experimental Procedures

Experiments begin with the selection of subjects. In naturalistic settings, subjects are often chosen opportunistically; however, to create relatively comparable situations across trials, it is advisable to use inclusion criteria that set behavioral standards and minimize distractions. Where possible, individually identifying subjects can prevent re-testing and allow for individual characteristics (e.g., demographic or reproductive characteristics) to be included in the analysis.

Stimuli are often presented via an apparatus that allows for their systematic presentation across trials. For example, photographs may be placed in frames covered by an occluder which can be lifted to reveal the stimuli at the appropriate time during the trial (e.g., Higham et al. 2011). Looking time experiments can use either sequential or simultaneous presentation of stimuli. In the former, each stimulus is presented singly, and looking times toward different stimuli are compared indirectly (e.g., Hughes et al. 2014). In the latter, stimuli are presented in groups (often pairs), so subjects can only look at one stimulus at a time (e.g., Higham et al. 2011). There are advantages and disadvantages to each of these approaches. The sequential approach makes it easier to assess gaze direction because gazes close to the camera are easier to recognize; however, variation in looking time between stimuli is hard to compare because the level of habituation to the task and circumstances surrounding stimuli presentation are not identical. While simultaneous presentation of stimuli facilitates the

comparison of looking time, precisely determining gaze direction can be challenging, especially in natural settings where other objects or events in the surroundings can attract the attention of subjects. In laboratory settings, this issue may be circumvented by the use of multiple video cameras and controlled surroundings. In field settings where a single camera is used, adequate spacing between stimuli is necessary to distinguish gazes directed toward each stimulus. At the same time, however, it becomes more difficult to recognize gazes aimed toward stimuli positioned further from the camera. In primates, we have found that an apparatus in which stimuli are separated by around one meter works well. Ultimately, the best presentation method will depend on the research question and the stimuli being presented. As in all experiments, order of presentation of stimuli should be randomized and counterbalanced. This is particularly important in looking time studies with simultaneous stimuli presentation because multiple species have been shown to exhibit a left gaze bias (Guo et al. 2009).

During stimuli presentation, experimental procedures and conditions should be as consistent as possible. For example, in field conditions, the apparatus should be placed similarly across trials such that the subject is within a specified distance, is equidistant from any simultaneously presented stimuli, is able to view each stimulus without turning their head more than a specified amount, and can view all stimuli under similar lighting conditions. In many cases, it is necessary to orient the subject to the locations of stimuli before they are displayed so that the direction of a gaze toward all stimuli can be identified on video, and this should also be done in a standardized fashion to reduce bias. In laboratory experiments in which light levels are changed during testing, subjects should be allowed to adapt fully to light levels in the test arena before testing begins (including those of a display monitor). For trials of captive individuals involving electronic presentation of stimuli, Fleishman & Endler (2000) recommend that subjects be presented with a display depicting the visual background against which stimuli will be viewed for 30 min before testing. When presenting naturalistic stimuli, brightness and contrast of the stimuli should match natural values (Fleishman & Endler 2000). Presenters should be blind to the condition of the trial, and decisions regarding the success or failure of each trial based on specified inclusion criteria should also be made blind to trial condition.

Many trials are videotaped so that they can be reviewed in greater detail at a later date, and to

facilitate coding of looking behavior; filming should therefore be performed in a way that facilitates later coding or other analysis. For example, the pupils must be visible in the video to determine the precise direction of eye gaze. While there may have been evolutionary selection on non-human primate eyes to decrease the ability of conspecifics to detect gaze (Kobayashi & Kohshima 1997), the direction of eye gaze is nonetheless usually readily identifiable with a relatively tight shot (e.g., including the head and shoulders) in good lighting (pers. obs.). If stimuli locations were determined at the beginning of the trial, it is important that the camera remains stationary throughout the trial to preserve this positional information. In trials in which the direction or zoom of the camera changes, it may be beneficial to re-orient the subject to the location of stimuli at the end of the trial, as this can help to determine the location of stimuli in the new video configuration. Videos should be recorded in a format compatible with coding software, as video conversion usually involves a loss of resolution.

Coding and Analysis

Differences in looking time between stimuli are usually stable and consistent, but also tend to be very small (often less than a second), making accurate coding of looking behavior essential. Most modern looking time studies measure eye gaze using either eye tracking technology or by manual coding of videos. Eye trackers sample eye gaze at a given interval (often 60 Hz) to identify visual fixation points, which are small regions (usually within 2–5 degrees of central vision) of the visual field that are the focus of sustained eye gaze for a minimum amount of time (usually 80–100 ms; Hansen & Ji 2010). The location and duration of each fixation point is then recorded to document the looking behavior of the subject. Eye tracking can be difficult to implement and, to our knowledge, has never been used in naturalistic conditions. Therefore, many studies rely on manual coding in which videos of each trial are usually coded frame by frame by a human observer. The first and last frames of the trial are identified based on standardized criteria, and each intermediate frame is coded based on the direction of eye gaze exhibited by the subject. Video coders should remain blind to the condition of each trial video, and intercoder reliability should always be assessed. Reliability scores should be based on initial similarities between coders, rather than scores obtained after extensive training aimed at increasing the similarity of measurements.

There are multiple analytical approaches that can be taken when analyzing looking time data. Many researchers (e.g., Waitt et al. 2003, 2006; Gerald et al. 2007) have assessed pooled looking times for each stimulus using traditional parametric statistical tests; however, when using this method, it is particularly important to assure that overall differences are not driven by a few strong preferences. Alternatively, comparisons can be made based on the number of individuals looking longest at each stimulus; however, in this case, very slight differences exhibited by many individuals may yield significant results. To avoid this, it may be appropriate to consider that a subject exhibited a visual bias only when the difference in looking time between stimuli is greater than a chosen threshold. Such differences can be established objectively by either testing the same image twice or using images depicting neutral stimuli lacking salience to the subject. The majority of studies using a looking time paradigm focus on relative looking duration as the primary outcome variable. However, there are many other variables that could also be examined, such as the direction of first gaze, latency to first gaze or to disengage, and the order of gaze directions (Bethell et al. 2012). Ultimately, the best way to analyze data will differ based on the goals of each individual study, and for some research questions, a combined approach may be most appropriate to confirm the patterns obtained.

Future Directions

When performed using careful methodology, analysis, and interpretation, studies based on the looking time experimental paradigm can be useful when addressing many different types of questions within the field of animal behavior, especially those related to perception and cognition. The recent expansion of these methods into field settings is an exciting development that seems likely to yield many new and interesting insights. Introducing looking time methods to new field sites and new species, including animal taxa other than primates, seems a logical next step. While each site and species will provide unique challenges, the general methods used to implement looking time tasks are likely to be adaptable to studying many species, particularly those that are well habituated and semiterrestrial. For non-habituated species, looking time tasks could still be used if movement patterns of individuals can be predicted or altered (e.g., by attracting subjects to study areas with food). A key benefit of the looking time experimental paradigm is that it allows for comparisons across both species and

contexts. Thus far few studies have capitalized on this advantage, however, and the expansion of looking time research into new contexts and new species should facilitate these comparisons.

One area of research in which looking time tasks are particularly relevant, but in which they are currently under-utilized, is the study of animal visual signals. Experiments using looking time methods could be used to address a wide variety of hypotheses, including those related to species and individual recognition, sexual selection, and crypsis. Some animal taxa may have developed color patterns that aid in the identification of conspecifics and thus help to maintain species boundaries (e.g., cichlids, Seehausen & van Alphen 1998; darters, Williams & Mendelson 2011; flycatchers, Saetre et al. 1997; guenons, Allen et al. 2014). Experiments could evaluate whether individuals discriminate between the visual signals displayed by conspecifics compared to those of closely related sympatric species. Similarly, they could help to identify the visual cues used to identify individual conspecifics. Second, many animal visual signals are also likely influenced by intraspecific sexual selection and could function in both intrasexual competition and intersexual mate choice (Andersson 1994). Many such signals have been identified in animal taxa based on behavioral correlations (Higham & Winters in press; Setchell in press), but very few have been subjected to experimental analysis. A notable exception is the research on visual signals conducted in rhesus macaques, and the successful implementation of looking time measures in this species highlights the value of this paradigm. Field experiments could help to illuminate the function of such signals in other species. Looking time methods could be useful in disentangling the effect of intra- and intersexual selection on the evolution of sexually selected traits in general, a task that is difficult to accomplish solely using behavioral observations (e.g., due to pronounced sexual coercion by males in many mammal species; Clutton-Brock & McAuliffe 2009). Experimental methodologies could also be used to determine whether the mate choice preferences of non-human primate females change across their menstrual cycle, as in humans (e.g., Penton-Voak & Perrett 2000). Finally, experiments could be used to assess the role of crypsis in animal coloration. Stimuli representing a given species could be presented to predators to determine the extent to which their colors and/or patterns reduce the likelihood of detection. This could be particularly useful when studying crypsis in taxa in which other types of experimental methods, such as those that expose subjects to predators, are not feasible.

Looking time tasks could also be used to address a number of additional questions in animal cognition. Numerous cognitive abilities have been studied, particularly in primates, but the developmental trajectory of these traits is not yet understood; looking time tasks could be used to better understand animal ontogeny. Both cross-sectional and longitudinal research using looking time tasks could help to understand the development of a wide range of cognitive abilities across taxa. For example, Mandalaywala et al. (2014) have recently documented the development of attentional bias toward threatening stimuli in rhesus macaques between 3 and 9 months of age, a phenomenon until then only reported for adults (Bethell et al. 2012); similar studies could be carried out assessing other cognitive capacities. Of particular interest could be potential changes in perception and motivation associated with the onset of sexual maturity. For instance, Dubuc et al. (in review) have recently shown that, as opposed to adults, juveniles do not show a visual bias toward dark red male faces, suggesting that such a bias is expressed only upon sexual maturity.

Looking time tasks should also be applied more broadly to non-primate taxa to better document cognitive abilities in other groups, which could be followed by questions related to ontogeny. For example, in the realm of social cognition, looking time tasks could also be used to assess the way animals view conspecifics. Research on ingroup–outgroup bias, the role of social relationships (e.g., kinship, dominance, affiliation) in animal societies, and the types of information that animals know about conspecifics could all be assessed using looking time methods. The implementation of this methodology across a wider range of taxa would help to facilitate comparative analyses that could identify broader evolutionary trends.

Multimodal communication in animals has recently received increased research focus (Partan & Marler 1999; Higham & Hebets 2013). Looking time tasks can be used to represent visual stimuli which are paired with corresponding stimuli from other modalities. Previous research has investigated the integration of audio playback and looking time tasks in this way (e.g., Ghazanfar & Logothetis 2003; Evans et al. 2005; Bovet & Deputte 2009; Silwa et al. 2011), with most results indicating that animals are sensitive to correspondences between auditory and visual stimuli and give stronger responses to corresponding stimuli. It would be interesting to assess the extent to which this pattern may be true for other combinations of modalities, such as the integration of visual and olfactory stimuli. Further research in this area will help shed

light on the ways in which animals integrate information from multiple signaling modalities.

A particularly interesting recent development has been the use of robotic animals in the study of animal behavior (Patricelli et al. 2002; Taylor et al. 2008; Karuse et al. 2011; Klein et al. 2012; Mitri et al. 2013). These robotic animals could be used as stimuli in looking time experiments, and have advantages over other classes of stimuli in that their appearance can be controlled and manipulated independently from their behavior, they are three dimensional, and they can move and 'behave' in a standardized fashion. To our knowledge, robotic stimuli have not yet been used in looking time tasks; however, they represent an intriguing possibility.

Conclusion

The looking time experimental paradigm was originally developed to research the perceptual and cognitive abilities of human infants, but has since been applied to a variety of animal species. Looking time tasks can be implemented across species and contexts, which makes this paradigm particularly useful in facilitating research on inter- and intraspecific variation. Such tasks can be used to study a variety of questions in animal behavior and cognition. While the looking time experimental paradigm has not been without criticism, it can nonetheless be a powerful methodology when executed and interpreted properly. The use of playback experiments to assess auditory signals in animals has been indispensable in understanding the information content of vocalizations, and the playback methodology has yielded a wide variety of insights into animal behavior and cognition (e.g., in primates, Cheney & Seyfarth 2007). The study of visual signals, which has thus far lagged behind that of auditory signals in many species, would benefit from the broader implementation of a similarly successful experimental methodology. The use of looking time tasks has begun to fill this void, and the application of these tasks to new questions and new species is likely to be successful. Like with any experimental methodology, looking tasks must be implemented with careful consideration of a number of factors; however, the expanded use of this paradigm is likely to be both feasible and fruitful.

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