



OPEN ACCESS

EDITED BY

Bernhard Hommel,
University Hospital Carl Gustav Carus, Germany

REVIEWED BY

Mario Dalmaso,
University of Padua, Italy

*CORRESPONDENCE

Vanessa A. D. Wilson
✉ vanessa.wilson@unine.ch

RECEIVED 18 January 2023

ACCEPTED 17 April 2023

PUBLISHED 02 May 2023

CITATION

Wilson VAD, Bethell EJ and Nawroth C (2023)
The use of gaze to study cognition: limitations,
solutions, and applications to animal welfare.
Front. Psychol. 14:1147278.
doi: 10.3389/fpsyg.2023.1147278

COPYRIGHT

© 2023 Wilson, Bethell and Nawroth. This is an open-access article distributed under the terms of the [Creative Commons Attribution License \(CC BY\)](https://creativecommons.org/licenses/by/4.0/). The use, distribution or reproduction in other forums is permitted, provided the original author(s) and the copyright owner(s) are credited and that the original publication in this journal is cited, in accordance with accepted academic practice. No use, distribution or reproduction is permitted which does not comply with these terms.

The use of gaze to study cognition: limitations, solutions, and applications to animal welfare

Vanessa A. D. Wilson^{1,2,3*}, Emily J. Bethell⁴ and Christian Nawroth⁵

¹Department of Comparative Cognition, Institute of Biology, University of Neuchâtel, Neuchâtel, Switzerland, ²Department of Comparative Language Science, University of Zurich, Zurich, Switzerland, ³Center for the Interdisciplinary Study of Language Evolution (ISLE), University of Zurich, Zurich, Switzerland, ⁴Research Centre in Evolutionary Anthropology and Palaeoecology, Liverpool John Moores University, Liverpool, United Kingdom, ⁵Institute of Behavioural Physiology, Research Institute for Farm Animal Biology (FBN), Dummerstorf, Germany

The study of gaze responses, typically using looking time paradigms, has become a popular approach to improving our understanding of cognitive processes in non-verbal individuals. Our interpretation of data derived from these paradigms, however, is constrained by how we conceptually and methodologically approach these problems. In this perspective paper, we outline the application of gaze studies in comparative cognitive and behavioral research and highlight current limitations in the interpretation of commonly used paradigms. Further, we propose potential solutions, including improvements to current experimental approaches, as well as broad-scale benefits of technology and collaboration. Finally, we outline the potential benefits of studying gaze responses from an animal welfare perspective. We advocate the implementation of these proposals across the field of animal behavior and cognition to aid experimental validity, and further advance our knowledge on a variety of cognitive processes and welfare outcomes.

KEYWORDS

looking time, attention, visual bias, animal behavior, social cognition, methodology, study design, welfare indicators

Introduction

Eye gaze is an implicit behavior that is used to determine visual attention, and provides a useful proxy measure of cognition, e.g., preferences, comprehension, knowledge, beliefs, and memory, in non-verbal subjects. Consequently, gaze measures such as gaze direction, looking time, anticipatory looking and gaze following, have become established tools in cognitive research (Tafreshi et al., 2014). Gaze measures have advanced our understanding of cognitive processes, but there are notable limitations. Despite calls in developmental psychology that caution about using gaze to understand higher-order cognition (Bogartz et al., 2000; Aslin, 2007; Tafreshi et al., 2014), gaze measures persist in this field, as well as in the study of animal cognition. In this perspective paper, we draw on literature both from developmental and comparative research. We focus on these fields, since methodological improvements with non-verbal subjects could lead to a better understanding of both the ontogenetic and the evolutionary origins of specific cognitive traits. Moreover, whilst these

fields both seek to answer similar questions regarding cognitive functions, and face similar methodological challenges, we suggest they could benefit from a broader exchange of ideas. Using examples from socio-cognitive studies utilizing gaze measures, we review the existing issues, propose solutions and improvements to existing methodologies, and address how we can give more consideration to the mechanisms that drive context-specific visual attention; we also discuss the general benefits, as well as future implementations, of a gaze-based approach for animal welfare related issues.

Using gaze to study cognition

Methods and applications

One of the most common approaches is the preferential looking paradigm—a method that compares length of time that gaze is directed toward different stimuli (images or videos). Stimuli are typically presented simultaneously as a pair, or individually at separate time points. Originally tested on an infant chimpanzee [*Pan troglodytes*, Fantz (1958a)] then with human infants (Fantz, 1958b), the method's simplicity and adaptability to different environments has made it popular amongst researchers working with animals. While indicating discrimination between stimuli (Koba and Izumi, 2008; Pfefferle et al., 2014), the goal of studies using this paradigm vary, with some aiming to uncover social orientations (Craighero et al., 2011; Franchini et al., 2017) or preferences (Paukner et al., 2017; Adams and Macdonald, 2018), recognition (Fujita, 1987; Schell et al., 2011; Méary et al., 2014; Rakotonirina et al., 2018) as well as memory for stimuli (Gothard et al., 2004; Howard et al., 2018) and shifts in underlying affective states (Bethell et al., 2012). The term *preferential looking* is synonymous with *looking time*, *attention*, and *gaze*. More recently the terms *visual bias* and *attention bias* have been introduced, most commonly for welfare studies where difference in looking duration to emotionally valenced stimulus pairs is measured (e.g., Crump et al., 2018).

A variation on the preferential looking paradigm is the “violation of expectation” (VoE) paradigm, where visual bias is interpreted as an indicator of surprise in response to something unexpected. VoE paradigms have been used to test expectations about visual perspectives (Arre et al., 2020), physical support violations (Baillargeon and Hanko-Summers, 1990; Cacchione and Krist, 2004; Perez and Feigenson, 2021), object motion (Spelke et al., 1994), and social violations, both in the visual (Rohr et al., 2015; Overduin-de Vries et al., 2016), and auditory domain (Cheney et al., 1995; Bergman et al., 2003; Slocombe et al., 2010).

The habituation/dishabituation paradigm is another adaptation of the preferential looking paradigm. Here, subjects are exposed to a stimulus until they reach a habituation response—measured through a decrease in looking time over multiple exposures—and are then exposed to a different stimulus. Their looking time is compared between the novel stimulus and the last habituation trial (Leslie, 1982). O'Connell and Dunbar (2005) measured perception of causality in chimpanzees using two different conditions. They showed either a probable scene (e.g., hand grasping a banana) followed by an improbable scene (e.g., banana moving on its

own) or an improbable followed by probable scene. Chimpanzees looked longer when viewing the improbable clip second (i.e., during dishabituation), but not when viewing the probable clip second, thereby suggesting that the improbable clip produced a causal violation. This approach has been used to study understanding of intention (Dasser et al., 1989) and vocal information (Rendall et al., 1996; Charlton et al., 2012; Baciadonna et al., 2019).

In contrast to the above approaches, anticipatory looking paradigms measure gaze direction prior to the onset of stimuli, providing information about expectations of event outcomes. This approach has been used to test predictions about goal-directed actions (Cannon and Woodward, 2012; Kano and Call, 2014) and related belief systems about object locations (Onishi and Baillargeon, 2005; Southgate et al., 2007; Krupenye et al., 2016).

Finally, gaze following paradigms test the ability to co-orient gaze with another individual (using cues from body, head, or eye orientation). Gaze following is a reflexive response that emerges during infancy (Deaner and Platt, 2003; Shepherd, 2010; Davidson and Clayton, 2016), and has been found in a range of taxonomic groups including reptiles (Wilkinson et al., 2010), birds (Schloegl et al., 2007), and mammals (Davidson and Clayton, 2016). In many birds and mammals, gaze following first emerges in response to the primary carer, suggesting it is a reflexive behavior facilitating behavioral coordination between infant and parent, enhancing learning opportunities (Schloegl et al., 2007; Davidson and Clayton, 2016). In human adults, gaze following is also mediated by multiple social variables (Dalmaso et al., 2020a), suggesting that gaze following is also integrated into less automated pathways for social processing (Shepherd, 2010). Similarly, in other species, evidence is also accumulating for more complex forms of gaze following, such as gaze following around barriers (Zeiträg et al., 2022).

Whilst the above paradigms are well established approaches, utilized both in lab settings and in free-ranging populations of non-human animals, all are inherently prone to conceptual and methodological issues which are often overlooked. In the following section, we outline these limitations and provide potential solutions.

Limitations to current methods

The primary issue with the above paradigms is in their interpretation of looking behavior. The preferential looking paradigm provides a simple yet effective way to determine discrimination between stimuli. The paradigm was originally developed to test discrimination between perceptual features, but was later adopted as an indicator of expectation or understanding (Tafreshi et al., 2014), and also as a means to assess shifts in underlying emotion (Paul et al., 2005; Bethell et al., 2012). It is through interpretive differences about underlying psychological and physiological states that this method becomes conceptually problematic. That is, preferential looking paradigms only demonstrate that a pair of stimuli can be discriminated, not why the stimuli are discriminated (Aslin, 2007; Tafreshi et al., 2014; Wilson et al., 2021). A study group might look longer at images of out-group members because to different individuals they are novel, threatening or attractive (Fujita, 1987; Méary et al., 2014). Or they might look longer at images of group members because they, again,

contain individually-relevant social information (Fujita, 1987; Dufour et al., 2006; Adams and Macdonald, 2018; Rakotonirina et al., 2018). If we don't know what exactly drives these visual biases, then evaluation in behavioral terms can be precarious and possibly misleading. Context, including the often-ignored factor of individual differences, is everything when it comes to interpretation (Wass, 2014).

From a broader perspective, it is paradoxical that the same response - visual bias - can varyingly be interpreted to indicate preference, interest, novelty, surprise or even levels of anxiety (Bethell et al., 2012; Tafreshi et al., 2014; Wilson et al., 2021); indeed, the use of the phrasing "preferential looking" is in itself misleading, as it imparts an element of choice in responses when they may be purely reflexive (Winters et al., 2015; Wilson et al., 2021). It also implies that visual bias is due to preference rather than avoidance. Such issues have already been raised in the field of infant cognition - Haith (1998) expresses concern for the use of gaze to make interpretations about higher order cognition, with perception-based explanations often being ignored (Bogartz et al., 2000).

A similar case is argued for the VoE paradigm, where a longer gaze is considered to indicate a surprise response. There are two issues here. The first is that, as pointed out above, the "meaning" of a visual bias is determined within the framework of the paradigm, so a longer looking time will only be considered to indicate surprise if a violation of expectation is being used. By comparison, a longer looking time in a different paradigm would not be interpreted as surprise, but as anything ranging from sexual attraction to threat-related attentional capture. Indeed, subjects may just be responding to novelty in the stimuli following familiarization trials (Wang, 2004). The second issue is that it is unclear what exactly should link a "surprise" response to an understanding of the expected outcome, especially in the absence of additional corroborating evidence (Tafreshi et al., 2014).

The habituation-dishabituation paradigm might provide one method to disentangle conflicting interpretations of visual bias. With a habituation phase followed by dishabituation, it is possible that the response to the dishabituation stimulus compared with the habituated one is due simply to the novelty of the new stimulus rather than any meaningful differentiation based on content. One way to deal with this is to add a re-habituation paradigm, where the initial sequence from the habituation trials is re-played after the dishabituation trial (Rendall et al., 1996). If change in response is not due only to change in stimulus, then response to the re-habituated stimulus should reflect the habituated response level. This approach may provide a way to determine whether subjects are simply distinguishing differences in low-level features, or whether they show consistent responses to particular stimulus categories.

Whilst conceptually more stable than the above measures, anticipatory looking is not without its limitations. A popular application of this measure is to predicting actions, and anticipatory gaze has been used to implicitly measure false belief understanding in infants (Southgate et al., 2007), apes (Krupenye et al., 2016), and Japanese macaques (*Macaca fuscata*) (Hayashi et al., 2020). Yet several studies have failed to replicate previous findings that infants implicitly understand false beliefs as measured through anticipatory looking (Dörrenberg et al., 2018; Kampis et al., 2021). This is not to say that predictive gaze is not a reliable measure, rather that it may be dependent on additional factors, such as

familiarity of action and agent (Elsner and Adam, 2021) as well as developmental variation, such that predictive gaze might not be a reliable measure for children under the age of 12 months (Daum et al., 2012). Given these complexities, robust interpretations with non-human subjects should rely on careful selection of test stimuli as well as inter-lab replication.

Earlier gaze following studies faced criticism primarily around issues of bias toward primates and anthropocentric interpretation in terms of visual perspective taking and Theory of Mind (van Rooijen, 2010). Subsequently, as research has embraced other taxonomic groups, interpretation has become more nuanced. Currently it is accepted that sensitivity to gaze in conspecifics (or human carers) and gaze following in general, can be innate and reflexive, and show a developmental trajectory (Schloegl et al., 2007; Zeiträg et al., 2022). Differentiation amongst these interpretations depends upon the experimental paradigm, but variation in methodologies has also made interspecific comparisons difficult (Zeiträg et al., 2022). In any case, gaze following appears to serve different functions across different species, varying from reflexive responses to visual perspective taking; it is therefore species-specific with respect to interpretation across a wide range of taxonomic groups (van Rooijen, 2010; Wilkinson et al., 2010; Leliveld et al., 2013; Davidson and Clayton, 2016).

An additional consideration is that different gaze measures may tap into different cognitive mechanisms. For example, Daum et al. (2012) proposes that a dissociation between infants' "online" measures such as predictive gaze and *post hoc* measures such as looking time could be due to different processing pathways when viewing goal-directed actions—one pathway processes goal location, the other goal identity. Alternatively, such differences may be due to processing state—predictive gaze relies on incomplete information, in contrast to *post hoc* measures, which respond to a completed action, and have more processing time. Together, such studies highlight that when measuring gaze, care is needed to account for perceptual, contextual, temporal and social variance before drawing interpretations about cognition.

Finally, confounding factors are known to influence experimental results. These may include (a) laterality effects; (b) habituation effects; (c) circadian and other timing effects. For example, in primates including humans, there is a right hemisphere superiority for emotional face processing (e.g., Lindell, 2013) which can result in differential looking patterns toward faces presented in the left versus right-visual-field (Howarth et al., 2021). Hemispheric specialization for visual processing has been demonstrated across invertebrate and vertebrate species (Rogers, 2014), with similarities and differences for emotional information (Leliveld et al., 2013). Laterality effects are therefore widespread and species-specific. Habituation to repeatedly shown stimuli (known as visual adaptation over the short term—seconds, minutes—and learning over longer time periods—hours, days, years) is a well documented neurological response to adapt to changes in the environment. Interest in test stimuli typically declines with repeated presentations, an effect which can be detected in gaze responses over just a few trials (Howarth et al., 2021). Circadian changes in alertness and arousal are also well documented across species, and in captivity these may be further influenced by husbandry procedures (Howarth et al., 2021). Confounds can be controlled for with careful experimental design, and through

inclusion as control variables and random effects in statistical analyses.

Solutions to current limitations

Experimental validation

Besides careful consideration of data interpretation, we encourage additional steps to improving the use of gaze measures to assess cognition. One option is to improve current methods through assessing measurement consistency. For example, attention in rhesus macaques (*Macaca mulatta*), measured as gaze duration to images of conspecific faces, showed high repeatability across a 4 year period, even when tested using different approaches [automated presentation compared with manually presented images (Howarth et al., 2021)]. Values fell above the average reported for behavioral trait repeatability ($R \sim 0.35$) (Bell et al., 2009) and were greater for viewing threat ($R = 0.63$) compared with neutral ($R = 0.39$) faces. Similarly, looking time in 11-month old infants correlated across different screen-based tasks, although not between screen-based and “live” viewing conditions (Wass, 2014). Perez and Feigenson (2021) also report individual repeatability in attention to a violation of expectation condition in infants across a 6 month period ($r = 0.38$). Correlation was not found for infants given an “expected” condition, suggesting that the violation of expectation measure tapped into more than just visual engagement with the stimuli. To address issues of novelty following familiarization trials in the violation of expectation paradigm, Wang (2004) presented 3–4 month old infants with an object permanence test without presenting a prior familiarization task. Infants looked longer in the incongruent (wide object fits behind narrow occluder) than congruent conditions (wide object fits behind wide occluder). In parallel, infants given a control condition comparison did not differentiate their visual attention (Wang, 2004). The author suggests that these findings rule out the possibility that infants’ visual responses are simply a result of habituation during the typical familiarization phase, that is, they are responding to more than just perceptual differences between the conditions.

A second consideration when accounting for gaze is not just the time spent looking toward a stimulus, but also the time spent looking away (Bethell et al., 2012; Rubio-Fernández, 2019). Whilst a subject might not continue to look toward a previously attended stimulus, they could still be processing it whilst looking elsewhere (i.e., the stimulus has captured their attention, neurologically speaking). Visual avoidance of threatening stimuli in humans can be characteristic of extreme anxiety, including phobia (Bögels and Mansell, 2004). More recently, the significance of visual avoidance of threat has been investigated in animals indicating some individuals may be prone to avoidant attentional profiles, especially when stressed (Bethell et al., 2012). Taking a more holistic approach to measuring gaze behavior could thereby provide a more complete picture of the different components of visual attention. Indeed, in studying attention to facial stimuli, averted gaze response should be considered for species who find direct gaze threatening (Coss et al., 2002; Morton et al., 2016).

A third option is to consider behavioral validation of gaze responses. In a task examining canine (*Canis familiaris*) help-seeking, Hirschi et al. (2022) differentiated potentially different meanings of gaze with time spent interacting with a food puzzle: They predicted that if human-directed gaze was an indication of social problem-solving, then it would be correlated with time spent interacting with the box. Alternatively, if gaze indicated giving up, then it would be negatively related to time spent on the box. Results indicated support for the former prediction. Visual engagement with a stimulus does also predict preference in forced choice tasks, for humans viewing facial images (Glaholt and Reingold, 2009) and long-tailed macaques (*Macaca fascicularis*) viewing non-social stimuli (Wilson et al., 2021). Matching visual stimuli with vocal stimuli may also help to identify “recognition” responses via incongruent cross-modal information (Sliwa et al., 2011; Albuquerque et al., 2016). Moreover, gaze responses from experiments can reflect real-world behavior: in 3- and 6-month old rhesus macaques, time spent looking at eye regions of facial images correlated with time spent interacting with peers as well as initiation of social interactions (Ryan et al., 2020).

Alternatively, studies might consider adding methods that do not rely on gaze. Approach latency (Morton et al., 2016; Wathan et al., 2016), frequency (Plimpton et al., 1981), forced choice approach (Cheries et al., 2008; Mascalzoni et al., 2010) and response-slowing tasks (Bethell et al., 2016) provide a simple way to measure response to social stimuli and may more directly reflect real-life decision-making. Forced-choice image discrimination has been trained in horses (*Equus ferus caballus*) (Lansade et al., 2020) and rainbow trout (*Oncorhynchus mykiss*) (Kleiber et al., 2021) as a way to test recognition. Examination of species-specific behavioral and physiological parameters, such as partner-specific displays (Satoh et al., 2016), emotional reactions (Plimpton et al., 1981), sexual receptivity (Clark and Uetz, 1993), changes in ear posture (Bellegarde et al., 2017), or changes in heart rate (Smith et al., 2016; Trösch et al., 2019) also provide informative approaches to understanding context-specific responses, such as recognition or preference. Incorporating such behavioral and physiological measures alongside gaze assessment would help to validate interpretations about visual bias in social contexts.

Investing in technological solutions

An alternative option in establishing interpretable gaze measures is the use of technological adaptations that allow more in-depth assessment of visual and behavioral responses. Eye tracking is an obvious choice for people working with captive animals, and in recent years advances in infra-red eye tracking have allowed for setups to track gaze in unrestrained primates (Hopper et al., 2020; Lewis and Krupenye, 2022) and trained dogs (Somppi et al., 2012; Kis et al., 2017; Abdai et al., 2021). Gaze studies have even been expanded beyond mammals (Winsor et al., 2021) to include birds (Kjærsgaard et al., 2008; Tyrrell et al., 2014), octopus (*Octopus bimaculoides*) (Taylor, 2020), and jumping spiders (*Phidippus audax*) (Jakob et al., 2018), although currently these methods still usually involve some kind of physical restraint, limiting natural behavioral responses. One consideration is that utilizing eye tracking does not necessarily avoid the issues outlined above,

such as ruling out perceptual explanations of gaze responses or identifying whether gaze is motivated by surprise, recognition, preference, or other factors. As with the previously discussed paradigms, eye tracking should utilize rigorous controls and clear linking hypotheses that justify why a given stimulus should elicit a given response (Aslin, 2007). For example, predictions grounded in ecologically relevant behaviors can help to disentangle attentional differences to stimuli, such as images of in-group versus out-group members (Brooks et al., 2022). Accounting for these issues, the benefits of eye tracking over “free viewing” paradigms are multifold.

Firstly, over and above free viewing studies, eye tracking can account for differences in eye movements when viewing a given stimulus. Eye movements can be divided into fixations and saccades. Fixations are when the eyes are fixed on one spot, allowing the viewer to acquire new information, whereas saccades are the movements between fixations; reduction in visual sensitivity means that information intake is restricted during saccades, but information processing still takes place (Irwin, 1998; Rayner, 2009). Notably, the fixation location does not necessarily reflect the point of cognitive focus, that is, a fixation does not necessarily indicate attention (Irwin, 2004). Additionally, eye movements, such as fixation duration and saccade length, also vary greatly between task types (Rayner, 2009). Eye tracking thus allows researchers the flexibility to choose the measures most suited to their research question, as well as task type. Eye tracking studies tend to fall into one of three classes: reflexive orienting, which can examine visual bias; voluntary saccades, used in studies where subjects are directed to look to a given stimulus; and spontaneous scan paths, which examine temporal gaze patterns, such as reading and scene exploration (Eckstein et al., 2017). All of these, in theory, could be used with non-verbal subjects, although voluntary saccades need time to develop in human infants (Eckstein et al., 2017) and a directed approach would require training with non-human animals.

Secondly, eye tracking allows one to assess not just whether a subject attends to one image more than another, but what features within that image are salient for those subjects. Comparative studies have revealed, for example, that when viewing faces, humans tend to fixate longer than non-human apes on the eye regions of faces (Dahl et al., 2009; Kano et al., 2012; Chertoff et al., 2018), and that when viewing goal-directed behavior, humans attend more to the faces of agents than chimpanzees (Myowa-Yamakoshi et al., 2012, 2015). Utilizing an understanding of species-specific viewing patterns could allow one to distinguish between gaze patterns that reflect different cognitive processes. For example, in humans, recognition of a stimulus can be achieved in just two fixations [e.g., Hsiao and Cottrell (2008)]. Exploration patterns (Eckstein et al., 2017; Coutrot et al., 2018) could be applied to account for responses within specific time windows - such as how subjects distribute attention to information within social scenes (Kano and Tomonaga, 2009; Webb et al., 2009; Nakano et al., 2010; McFarland et al., 2013) and identifying anticipatory responses in action sequences (Kano and Call, 2014; Kano and Hirata, 2015; Krupenye et al., 2016).

Finally, this approach offers additional measures beyond gaze location that could be informative for studying cognition. One of these is pupil dilation, which may complement looking time measures (Jackson and Sirois, 2009). Whilst pupil diameter is light sensitive, changes to pupil size under consistent luminance can provide a measure of cognitive load, attention and arousal

(Beatty, 1982; Karatekin, 2004; Bradley et al., 2008). In preferential looking time paradigms and violation of expectation studies, measuring pupil size alongside gaze could help researchers to distinguish possible explanations for visual bias. For example, pupil dilation has been found in response to expectation violation in infants (Sirois and Jackson, 2012; Dörrenberg et al., 2018) and to motion violations in dogs (Völter and Huber, 2022), and is indicative of emotional arousal in a helping task in chimpanzees (Hepach et al., 2021). Pupillometry has also been used in chimpanzees to examine pupil-mimicry (Kret et al., 2014), and given varied applications in human research (Eckstein et al., 2017) has the potential to be applied more broadly in cognitive research with non-human subjects. Similar to pupil diameter, microsaccades, which are small saccades produced during gaze fixation (as opposed to saccades, which are produced between gaze fixations) (Martinez-Conde et al., 2013), may provide an indication of cognitive load. For example, when adult humans are instructed to prepare to look away from a target (instead of toward it), they produce fewer microsaccades, and a larger pupil size, although only when presented with mixed trial types (Dalmaso et al., 2020b). Microsaccades can also be informative to gaze orientation, with applications to gaze following studies (Deaner and Platt, 2003). A third, and less explored possibility, is that of blink rate. Blink rate may act as an indirect measure of dopamine activity (Jongkees and Colzato, 2016; Eckstein et al., 2017), a neurotransmitter that is important for “cognitive effort” such as executive function, learning, and decision-making (Westbrook and Braver, 2016). Blink rate is linked to cognitive flexibility in humans (Eckstein et al., 2017), and in Japanese macaques decreases during grooming compared to resting states, suggesting concentration (Hikida, 2022). In rhesus macaques, it has been shown to change in response to presentation of social and emotional information (Ballesta et al., 2016), and increased blink rate is correlated with group size across 71 primate species (Tada et al., 2013). These studies suggest that it may provide a useful measure in the assessment of socio-cognitive traits with non-human primates. Notably, the latter two studies coded blink rate from video footage of faces, indicating that this measure can also be assessed in completely natural settings.

Beyond eye tracking, Artificial Intelligence offers a new set of technological tools to measure gaze from high quality digital images. This would allow high throughput, instantaneously extracting information in near-real-time, and achieving accuracy comparable to human coders (Mathis et al., 2018). Machine Learning algorithms now exist for identifying individuals by their facial characteristics in facially heterogeneous species ranging from birds (Ferreira et al., 2020) to primates (Witham, 2018) and online databases are becoming available [e.g., DeepLabCut Model Zoo: Mathis et al. (2018)]. Within macaque faces, it is possible to landmark facial features such as eyes and pupils (Witham, 2018; Bethell et al., 2022) which, when triangulated with other metrics such as head pose and stimulus location, show promise for assessing direction of gaze with respect to known stimuli (Bethell et al., 2022). It is early days for the application of Machine Learning approaches to eye gaze detection, even in humans where resources are most heavily invested for commercial application (e.g., Khan et al., 2020), and currently initial image gathering, labeling and training is time consuming for each new application. As Machine Learning becomes more widespread there are likely to

be substantial developments in the coming years that will improve the efficacy of these approaches for work with animals.

Collaborative research

Historically, laboratories have aimed to standardize their tests, characteristics of test subjects, and environmental conditions to minimize variability. However, it can be argued that these standardization efforts create results that are vulnerable to site- and population-specific idiosyncrasies and make reproducing them difficult (Würbel, 2000; Voelkl et al., 2018). In contrast, a multi-site approach values data heterogeneity and accounts for intra-specific variation. Consequently, human psychological research was the first to adapt such an approach to improve reproducibility and applicability in their respective research field (e.g., Many Labs, ManyBabies), while initiatives in non-human species have started to follow suit (e.g., ManyPrimates et al., 2019; Lambert et al., 2022; ManyDogs Project et al., 2022). Such multi-lab approaches can also help to facilitate interdisciplinary work between researchers of different fields (e.g., developmental and comparative) to help advance methodological issues. For example, studies examining questions that branch both comparative and development approaches, such as the uncanny valley effect (Mori et al., 2012; Brink et al., 2019; Siebert et al., 2020; Wilson et al., 2020; Carp et al., 2022; Diel et al., 2022) or Theory of Mind (Krupenye et al., 2016; Buttelmann et al., 2017; Dörrenberg et al., 2018), could benefit from more unity between these fields.

Benefits to research and welfare applications

Study design and animal welfare

Decision-making tasks are often used to investigate the perceptive and cognitive processes of non-human animals. There are, however, pitfalls: during these tasks, animals often undergo potentially stressful prolonged habituation and training. This can impact individual performance in subsequent experimental tasks via a potential decrease of motivation to participate. For example, tasks that require extensive training may result in self-selected samples where some animals are intrinsically motivated to work or find the tasks enriching, while others might struggle to learn the task contingencies or lack dexterity for manual responses. Prolonged, and potentially stressful, training and isolation can also impact on an individual's learning performance (Mendl et al., 1997). Moreover, this is also relevant in terms of the implementation of the 3Rs principle as it can severely impact the welfare of the tested animals due to the stress they are experiencing (Refinement).

Assessing gaze as a measure of attention to specific stimuli might be a more beneficial approach, in terms of the ecological validity of the data that will be collected and the animals that are subjected to the tasks. Gaze duration paradigms that utilize biologically relevant stimuli have the advantage that they are not based on excessive training regimes (e.g., used to shape a subject's behavior to indicate a choice), anatomical endowments

(for example, the presence of hands), or specific motor abilities (e.g., needed in manipulating a device). Assessing gaze has the additional advantage that it does not rely on individually learned behavioral responses (i.e., training), so animals can be repeatedly tested in several similar test series as no carry-over learning bias will occur – additionally improving a better incorporation of the 3Rs principle in animal research (Reduction).

These outlined points might be particularly relevant when we want to assess the cognitive capacities of prey animal species. Prey animals usually pay increased visual attention to potentially dangerous situations. Looking time measures could be used to capture this so-called startle response, a reaction shown by many prey species, such as ungulates, where their attention becomes fixated on novel (and thus potentially threatening) stimuli. With higher alert behavior and, thus, stress levels, prey animals might also benefit from reduced time spent in isolation for habituation and training purposes. Welfare-wise, this approach would be of particular relevance when we want to assess the wellbeing of animals kept under human care - with many of them being prey species (not only in farms, but also in zoos).

Gaze measures as indicators of welfare

One advantage of using gaze as a behavioral measure is that it may directly reflect individual differences in fundamental aspects of social cognition such as interest, motivation, emotional disposition as well as more subtle aspects such as fearfulness, avoidance and depression. This could be especially useful for identifying animals most “at risk” for compromised welfare, allowing for pre-emptive management interventions. For example, lack of visual attention to events in the social group is a partial diagnostic criteria for depressive-like behavior in primate models of depression (Shively and Willard, 2012). Methods to identify early signs of reduced visual scanning could help alert care staff to individuals suffering within the current environment.

In humans, cognitive models of emotion reveal that visual attention toward biologically relevant stimuli (such as emotional faces) varies with underlying emotion. People who are anxious become overly attentive to threat cues, while phobics may go to extremes to avoid phobia-related stimuli altogether. This well established relationship between emotions like anxiety and attention—measured either as gaze duration or reaction times (e.g., on the dot probe task)—is supported by a large body of literature (Bar-Haim et al., 2007). Similarly, rhesus macaques tested at a 4 year interval showed high repeatability for duration of gaze toward pictures of threatening conspecific faces (Howarth et al., 2021), with a few individuals avoiding threat faces altogether (shortest look duration = 0 ms) and others spending most of the 3 s trial looking toward the threat face (longest look duration = 2,912 ms). Extremes of attention toward (or away from) threat may be associated with underlying anxiety which, if chronically elevated, poses a welfare concern (Bethell et al., 2012). Attention bias tasks have been proposed as a non-invasive tool that could be applied to distinguish acute from chronic anxiety across taxonomic groups (Crump et al., 2018).

Sensitivity to gaze may also be an important consideration for management of animals in captivity, either because prey species

may be highly sensitive to direct gaze from humans or because social species are sensitive to the gaze of conspecifics (Davidson and Clayton, 2016). Providing visual barriers that allow animals to avoid direct gaze from both humans and conspecifics is a fundamental enrichment refinement for socially housed and/or prey species where direct gaze may be perceived as a threat (Reinhardt, 2004).

Conclusion

There are multiple approaches to, and applications of, measuring gaze to study animal and infant cognition. Whilst we caution for better experimental controls and more robust validation of these approaches, we also advocate the use of gaze measures under careful interpretation, proposing solutions that can avoid common pitfalls associated with this methodology. In addition, the use of gaze measurements could be beneficial when accounting for animal welfare, by providing a low-impact approach to testing, and could also be useful as a welfare indicator. Moreover, advances in technology and collaborative research have the potential to open the door for large-scale, robust and non-invasive cognitive testing of a wide range of species.

Data availability statement

The original contributions presented in this study are included in the article/supplementary material, further inquiries can be directed to the corresponding author.

References

- Abdai, J., Ferdinandy, B., Lengyel, A., and Miklósi, Á. (2021). Animacy perception in dogs (*Canis familiaris*) and humans (*Homo sapiens*): comparison may be perturbed by inherent differences in looking patterns. *J. Comp. Psychol.* 135, 82–88. doi: 10.1037/com0000250
- Adams, L. C., and Macdonald, S. E. (2018). Spontaneous preference for primate photographs in Sumatran orangutans (*Pongo abelii*). *Int. J. Comp. Psychol.* 31, 1–16. doi: 10.46867/ijcp.2018.31.04.05
- Albuquerque, N., Guo, K., Wilkinson, A., Savalli, C., Otta, E., and Mills, D. (2016). Dogs recognize dog and human emotions. *Biol. Lett.* 12:20150883. doi: 10.1098/rsbl.2015.0883
- Arre, A. M., Clark, C. S., and Santos, L. R. (2020). Do young rhesus macaques know what others see? A comparative developmental perspective. *Am. J. Primatol.* 82:e23054. doi: 10.1002/ajp.23054
- Aslin, R. N. (2007). What's in a look? *Dev. Sci.* 10, 48–53. doi: 10.1111/j.1467-7687.2007.00563.x
- Baciadonna, L., Briefer, E. F., Favaro, L., and McElligott, A. G. (2019). Goats distinguish between positive and negative emotion-linked vocalisations. *Front. Zool.* 16:25. doi: 10.1186/s12983-019-0323-z
- Baillargeon, R., and Hanko-Summers, S. (1990). Is the top object adequately supported by the bottom object? Young infants' understanding of support relation. *Cogn. Dev.* 5, 29–53.
- Ballesta, S., Mosher, C. P., Szep, J., Fischl, K. D., and Gothard, K. M. (2016). Social determinants of eyeblinks in adult male macaques. *Sci. Rep.* 6:38686. doi: 10.1038/srep38686
- Bar-Haim, Y., Lamy, D., Pergamin, L., Bakermans-Kranenburg, M. J., and van IJzendoorn, M. H. (2007). Threat-related attentional bias in anxious and nonanxious individuals: a meta-analytic study. *Psychol. Bull.* 133, 1–24. doi: 10.1037/0033-2909.133.1.1
- Beatty, J. (1982). Task-evoked pupillary responses, processing load, and the structure of processing resources. *Psychol. Bull.* 91, 276–292.
- Bell, A. M., Hankison, S. J., and Laskowski, K. L. (2009). The repeatability of behaviour: a meta-analysis. *Anim. Behav.* 77, 771–783. doi: 10.1016/j.anbehav.2008.12.022
- Bellegarde, L. G. A., Haskell, M. J., Duvaux-ponter, C., Weiss, A., Boissy, A., and Erhard, H. W. (2017). Face-based perception of emotions in dairy goats. *Appl. Anim. Behav. Sci.* 193, 51–59. doi: 10.1016/j.applanim.2017.03.014
- Bergman, T. J., Beehner, J. C., Cheney, D. L., and Seyfarth, R. M. (2003). Hierarchical classification by rank and kinship in baboons. *Science* 302, 1234–1236. doi: 10.1126/science.1087513
- Bethell, E. J., Holmes, A., MacLarnon, A., and Semple, S. (2012). Evidence that emotion mediates social attention in rhesus macaques. *PLoS One* 7:e44387. doi: 10.1371/journal.pone.0044387
- Bethell, E. J., Holmes, A., Maclarnon, A., and Semple, S. (2016). Emotion evaluation and response slowing in a non-human primate: new directions for cognitive bias measures of animal emotion? *Behav. Sci.* 6, 1–16. doi: 10.3390/bs6010002
- Bethell, E. J., Khan, W., and Hussain, A. (2022). A deep transfer learning model for head pose estimation in rhesus macaques during cognitive tasks: towards a nonrestraint noninvasive 3Rs approach. *Appl. Anim. Behav. Sci.* 255:105708. doi: 10.1016/j.applanim.2022.105708
- Bogartz, R. S., Shinsky, J. L., and Schilling, T. H. (2000). Object permanence in five-and-a-half-month-old infants? *Infancy* 1, 403–428. doi: 10.1207/S15327078IN0104_3
- Bögels, S. M., and Mansell, W. (2004). Attention processes in the maintenance and treatment of social phobia: hypervigilance, avoidance and self-focused attention. *Clin. Psychol. Rev.* 24, 827–856. doi: 10.1016/j.cpr.2004.06.005
- Bradley, M. M., Miccoli, L., Escrig, M. A., and Lang, P. J. (2008). The pupil as a measure of emotional arousal and autonomic activation. *Psychophysiology* 45, 602–607. doi: 10.1111/j.1469-8986.2008.00654.x

Author contributions

VW: conceptualization, writing—original draft preparation, and writing—reviewing and editing. EB and CN: conceptualization and writing—reviewing and editing. All authors contributed to the article and approved the submitted version.

Funding

Open access funding by University of Neuchâtel.

Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

All claims expressed in this article are solely those of the authors and do not necessarily represent those of their affiliated organizations, or those of the publisher, the editors and the reviewers. Any product that may be evaluated in this article, or claim that may be made by its manufacturer, is not guaranteed or endorsed by the publisher.

- Brink, K. A., Gray, K., and Wellman, H. M. (2019). Creepiness creeps in: uncanny valley feelings are acquired in childhood. *Child Dev.* 90, 1202–1214. doi: 10.1111/cdev.12999
- Brooks, J., Kano, F., Kawaguchi, Y., and Yamamoto, S. (2022). Oxytocin promotes species-relevant outgroup attention in bonobos and chimpanzees. *Horm. Behav.* 143:105182. doi: 10.1016/j.yhbeh.2022.105182
- Buttelmann, D., Buttelmann, F., Carpenter, M., Call, J., and Tomasello, M. (2017). Great apes distinguish true from false beliefs in an interactive helping task. *PLoS One* 12:e0173793. doi: 10.1371/journal.pone.0173793
- Cacchione, T., and Krist, H. (2004). Recognizing impossible object relations: intuitions about support in chimpanzees (*Pan troglodytes*). *J. Comp. Psychol.* 118, 140–148. doi: 10.1037/0735-7036.118.2.140
- Cannon, E. N., and Woodward, A. L. (2012). Infants generate goal-based action predictions. *Dev. Sci.* 15, 292–298. doi: 10.1111/j.1467-7687.2011.01127.x
- Carp, S. B., Santistevan, A. C., Machado, C. J., Whitaker, A. M., Aguilar, B. L., and Bliss-Moreau, E. (2022). Monkey visual attention does not fall into the uncanny valley. *Sci. Rep.* 12:11760. doi: 10.1038/s41598-022-14615-x
- Charlton, B. D., Ellis, W. A. H., Larkin, R., and Tecumseh Fitch, W. (2012). Perception of size-related formant information in male koalas (*Phascolarctos cinereus*). *Anim. Cogn.* 15, 999–1006. doi: 10.1007/s10071-012-0527-5
- Cheney, D. L., Seyfarth, R. M., and Silk, J. B. (1995). The responses of female baboons (*Papio cynocephalus ursinus*) to anomalous social interactions: evidence for causal reasoning? *J. Comp. Psychol.* 109, 134–141. doi: 10.1037/0735-7036.109.2.134
- Cheries, E. W., Mitroff, S. R., Wynn, K., and Scholl, B. J. (2008). Cohesion as a principle of object persistence in infancy. *Dev. Sci.* 11, 427–432. doi: 10.1111/j.1467-7687.2008.00687.x
- Chertoff, S., Margulis, S., and Rodgers, J. D. (2018). Visual processing of faces in juvenile western lowland gorillas without the use of training or reinforcement: a pilot study. *Anim. Behav. Cogn.* 5, 292–299. doi: 10.26451/abc.05.03.04.2018
- Clark, D. L., and Uetz, G. W. (1993). Signal efficacy and the evolution of male dimorphism in the jumping spider, *Maevia inclemens*. *Proc. Natl. Acad. Sci. U.S.A.* 90, 11954–11957. doi: 10.1073/pnas.90.24.11954
- O'Connell, S., and Dunbar, R. I. M. (2005). The perception of causality in chimpanzees (*Pan spp.*). *Anim. Cogn.* 8, 60–66. doi: 10.1007/s10071-004-0231-1
- Coss, R. G., Marks, S., and Ramakrishnan, U. (2002). Early environment shapes the development of gaze aversion by wild bonnet macaques (*Macaca radiata*). *Primates* 43, 217–222. doi: 10.1007/BF02629649
- Coutrot, A., Hsiao, J. H., and Chan, A. B. (2018). Scanpath modeling and classification with hidden Markov models. *Behav. Res. Methods* 50, 362–379. doi: 10.3758/s13428-017-0876-8
- Craighero, L., Leo, I., Umiltà, C., and Simion, F. (2011). Newborns' preference for goal-directed actions. *Cognition* 120, 26–32. doi: 10.1016/j.cognition.2011.02.011
- Crump, A., Arnott, G., and Bethell, E. J. (2018). Affect-driven attention biases as animal welfare indicators: review and methods. *Animals* 8:136. doi: 10.3390/ani8080136
- Dahl, C. D., Wallraven, C., Bühlhoff, H. H., and Logothetis, N. K. (2009). Humans and macaques employ similar face-processing strategies. *Curr. Biol.* 19, 509–513. doi: 10.1016/j.cub.2009.01.061
- Dalmaso, M., Castelli, L., and Galfano, G. (2020a). Social modulators of gaze-mediated orienting of attention: a review. *Psychon. Bull. Rev.* 27, 833–855. doi: 10.3758/s13423-020-01730-x
- Dalmaso, M., Castelli, L., and Galfano, G. (2020b). Microsaccadic rate and pupil size dynamics in pro-/anti-saccade preparation: the impact of intermixed vs. blocked trial administration. *Psychol. Res.* 84, 1320–1332. doi: 10.1007/s00426-018-01141-7
- Dasser, V., Ulbaek, I., and Premack, D. (1989). The perception of intention. *Science* 243, 365–367. doi: 10.1126/science.2911746
- Daum, M. M., Attig, M., Gunawan, R., Prinz, W., and Gredebäck, G. (2012). Actions seen through babies' eyes: a dissociation between looking time and predictive gaze. *Front. Psychol.* 3:370. doi: 10.3389/fpsyg.2012.00370
- Davidson, G. L., and Clayton, N. S. (2016). New perspectives in gaze sensitivity research. *Learn. Behav.* 44, 9–17. doi: 10.3758/s13420-015-0204-z
- Deaner, R. O., and Platt, M. L. (2003). Reflexive social attention in monkeys and humans. *Curr. Biol.* 13, 1609–1613. doi: 10.1016/j.cub.2003.08.025
- Diel, A., Weigelt, S., and Macdorman, K. F. (2022). A meta-analysis of the uncanny valley's independent and dependent variables. *ACM Trans. Hum. Robot Interact.* 11, 1–33. doi: 10.1145/3470742
- Dörrenberg, S., Rakoczy, H., and Liszkowski, U. (2018). How (not) to measure infant Theory of Mind: testing the replicability and validity of four non-verbal measures. *Cogn. Dev.* 46, 12–30. doi: 10.1016/j.cogdev.2018.01.001
- Dufour, V., Pascalis, O., and Petit, O. (2006). Face processing limitation to own species in primates, a response to social needs? *Behav. Processes* 73, 107–113. doi: 10.1016/j.beproc.2006.04.006
- Eckstein, M. K., Guerra-Carrillo, B., Miller Singley, A. T., and Bunge, S. A. (2017). Beyond eye gaze: what else can eyetracking reveal about cognition and cognitive development? *Dev. Cogn. Neurosci.* 25, 69–91. doi: 10.1016/j.dcn.2016.11.001
- Elsner, B., and Adam, M. (2021). Infants' goal prediction for simple action events: the role of experience and agency cues. *Top. Cogn. Sci.* 13, 45–62. doi: 10.1111/tops.12494
- Fantz, R. L. (1958a). Visual discrimination in a neonate chimpanzee. *Percept. Mot. Skills* 8, 59–66.
- Fantz, R. L. (1958b). Pattern vision in young infants. *Psychol. Rec.* 8, 43–47.
- Ferreira, A. C., Silva, L. R., Renna, F., Brandl, H. B., Renoult, J. P., Farine, D. R., et al. (2020). Deep learning-based methods for individual recognition in small birds. *Methods Ecol. Evol.* 11, 1072–1085. doi: 10.1111/2041-210X.13436
- Franchini, M., Glaser, B., de Wilde, H. W., Gentaz, E., Eliez, S., and Schaer, M. (2017). Social orienting and joint attention in preschoolers with autism spectrum disorders. *PLoS One* 12:e0178859. doi: 10.1371/journal.pone.0178859
- Fujita, K. (1987). Species recognition by five macaque monkeys. *Primates* 28, 353–366.
- Glaholt, M. G., and Reingold, E. M. (2009). Predicting preference from fixations. *PsychNology J.* 7, 141–158. doi: 10.1037/e527342012-455
- Gothard, K. M., Erickson, C. A., and Amaral, D. G. (2004). How do rhesus monkeys (*Macaca mulatta*) scan faces in a visual paired comparison task? *Anim. Cogn.* 7, 25–36. doi: 10.1007/s10071-003-0179-6
- Haith, M. M. (1998). Who put the cog in infant cognition? Is rich interpretation too costly? *Infant Behav. Dev.* 21, 167–179. doi: 10.1016/S0163-6383(98)90001-7
- Hayashi, T., Akikawa, R., Kawasaki, K., Egawa, J., Minamimoto, T., Koboyashi, K., et al. (2020). Macaques exhibit implicit gaze bias anticipating others' false-belief-driven actions via medial prefrontal cortex article. *Cell Rep.* 30, 4433–4444. doi: 10.1016/j.celrep.2020.03.013
- Hepach, R., Vaish, A., Kano, F., Albiach-Serrano, A., Benzriad, L., Call, J., et al. (2021). Chimpanzees' (*Pan troglodytes*) internal arousal remains elevated if they cannot themselves help a conspecific. *J. Comp. Psychol.* 135, 196–207. doi: 10.1037/com0002255
- Hikida, K. (2022). Eyeblick rate as an indicator of concentration on grooming in Japanese macaques (*Macaca fuscata*). *Am. J. Primatol.* 84:e23392. doi: 10.1002/ajp.23392
- Hirschi, A., Mazzini, A., and Riemer, S. (2022). Disentangling help-seeking and giving up: differential human-directed gazing by dogs in a modified unsolvable task paradigm. *Anim. Cogn.* 25, 821–836. doi: 10.1007/s10071-021-01595-0
- Hopper, L. M., Gulli, R. A., Howard, L. H., Kano, F., Krupenye, C., Ryan, A. M., et al. (2020). The application of noninvasive, restraint-free eye-tracking methods for use with nonhuman primates. *Behav. Res. Methods* 53, 1003–1030. doi: 10.3758/s13428-020-01465-6
- Howard, L. H., Festa, C., Lonsdorf, E. V., and College, M. (2018). Through their eyes: the influence of social models on attention and memory in capuchin monkeys (*Sapajus apella*). *J. Comp. Psychol.* 132, 210–219. doi: 10.1037/com0000111
- Howarth, E. R. I., Kemp, C., Thatcher, H. R., Szott, I. D., Farningham, D., Witham, C. L., et al. (2021). Developing and validating attention bias tools for assessing trait and state affect in animals: a worked example with *Macaca mulatta*. *Appl. Anim. Behav. Sci.* 234:105198. doi: 10.1016/j.applanim.2020.105198
- Hsiao, J. H., and Cottrell, G. (2008). Two fixations suffice in face recognition. *Psychol. Sci.* 19, 998–1006. doi: 10.1111/j.1467-9280.2008.02191.x
- Irwin, D. E. (1998). Lexical processing during saccadic eye movements. *Cognit. Psychol.* 36, 1–27.
- Irwin, D. E. (2004). "Fixation location and fixation duration as indices of cognitive processing," in *The interface of language, vision and action: eye movements and the visual world*, eds J. M. Henderson and F. Ferreira (New York, NY: Psychology Press), 105–134.
- Jackson, I., and Sirois, S. (2009). Infant cognition: going full factorial with pupil dilation. *Dev. Sci.* 12, 670–679. doi: 10.1111/j.1467-7687.2008.00805.x
- Jakob, E. M., Long, S. M., Harland, D. P., Jackson, R. R., Carey, A., Searles, M. E., et al. (2018). Lateral eyes direct principal eyes as jumping spiders track objects. *Curr. Biol.* 28, R1092–R1093. doi: 10.1016/j.cub.2018.07.065
- Jongkees, B. J., and Colzato, L. S. (2016). Spontaneous eye blink rate as predictor of dopamine-related cognitive function—A review. *Neurosci. Biobehav. Rev.* 71, 58–82. doi: 10.1016/j.neubiorev.2016.08.020
- Kampis, D., Kármán, P., Csibra, G., Southgate, V., and Hernik, M. (2021). A two-lab direct replication attempt of Southgate, Senju and Csibra (2007). *R. Soc. Open Sci.* 8:210190. doi: 10.1098/rsos.210190
- Kano, F., and Call, J. (2014). Great apes generate goal-based action predictions: an eye-tracking study. *Psychol. Sci.* 25, 1691–1698. doi: 10.1177/0956797614536402
- Kano, F., and Hirata, S. (2015). Great apes make anticipatory looks based on long-term memory of single events. *Curr. Biol.* 25, 2513–2517. doi: 10.1016/j.cub.2015.08.004

- Kano, F., and Tomonaga, M. (2009). How chimpanzees look at pictures: a comparative eye-tracking study. *Proc. Biol. Sci.* 276, 1949–1955. doi: 10.1098/rspb.2008.1811
- Kano, F., Call, J., and Tomonaga, M. (2012). Face and eye scanning in gorillas (*Gorilla gorilla*), orangutans (*Pongo abelii*), and humans (*Homo sapiens*): unique eye-viewing patterns in humans among hominids. *J. Comp. Psychol.* 126, 388–398. doi: 10.1037/a0029615
- Karatekin, C. (2004). Development of attentional allocation in the dual task paradigm. *Int. J. Psychophysiol.* 52, 7–21. doi: 10.1016/j.ijpsycho.2003.12.002
- Khan, W., Hussain, A., Kuru, K., and Al-askar, H. (2020). Pupil localisation and eye centre estimation using machine learning and computer vision. *Sensors* 20:3785. doi: 10.3390/s20133785
- Kis, A., Hernádi, A., Miklósi, B., Kanizsár, O., and Topál, J. (2017). The way dogs (*canis familiaris*) look at human emotional faces is modulated by oxytocin. An eye-tracking study. *Front. Behav. Neurosci.* 11:210. doi: 10.3389/fnbeh.2017.00210
- Kjærsgaard, A., Pertoldi, C., Loeschcke, V., and Witzner, H. D. (2008). Tracking the gaze of birds. *J. Avian Biol.* 39, 466–469. doi: 10.1111/j.2008.0908-8857.04288.x
- Kleiber, A., Valotaire, C., Patinote, A., Sudan, P.-L., Gourmelen, G., Duret, C., et al. (2021). Rainbow trout discriminate 2-D photographs of conspecifics from distracting stimuli using an innovative operant conditioning device. *Learn. Behav.* 49, 292–306. doi: 10.3758/s13420-020-00453-2
- Koba, R., and Izumi, A. (2008). Japanese monkeys (*Macaca fuscata*) discriminate between pictures of conspecific males and females without specific training. *Behav. Processes* 79, 70–73. doi: 10.1016/j.beproc.2008.04.005
- Kret, M. E., Tomonaga, M., and Matsuzawa, T. (2014). Chimpanzees and humans mimic pupil-size of conspecifics. *PLoS One* 9:e104886. doi: 10.1371/journal.pone.0104886
- Krupenye, C., Kano, F., Hirata, S., Call, J., and Tomasello, M. (2016). Great apes anticipate that other individuals will act according to false beliefs. *Science* 354, 110–114. doi: 10.1126/science.aa8110
- Lambert, M., Farrar, B., Garcia-Pelegri, E., Reber, S., and Miller, R. (2022). ManyBirds: a multi-site collaborative Open Science approach to avian cognition and behavior research. *Anim. Behav. Cogn.* 9, 133–152. doi: 10.26451/abc.09.01.11.2022
- Lansade, L., Colson, V., Parias, C., Trösch, M., Reigner, F., and Calandrea, L. (2020). Female horses spontaneously identify a photograph of their keeper, last seen six months previously. *Sci. Rep.* 10:6302. doi: 10.1038/s41598-020-62940-w
- Leliveld, L. M. C., Langbein, J., and Puppe, B. (2013). The emergence of emotional lateralization: evidence in non-human vertebrates and implications for farm animals. *Appl. Anim. Behav. Sci.* 145, 1–14. doi: 10.1016/j.applanim.2013.02.002
- Leslie, A. M. (1982). The perception of causality in infants. *Perception* 11, 173–186.
- Lewis, L. S., and Krupenye, C. (2022). Eye-tracking as a window into primate social cognition. *Am. J. Primatol.* 84:e23393. doi: 10.1002/ajp.23393
- Lindell, A. (2013). Continuities in emotion lateralization in human and non-human primates. *Front. Hum. Neurosci.* 7. doi: 10.3389/fnhum.2013.00464
- ManyDogs Project, Alberghina, D., Bray, E. E., Buchsbaum, D., Byosiere, S.-E., Espinosa, J., et al. (2022). ManyDogs project: a big team science approach to investigating canine behavior and cognition. *PsyArxiv* [preprint] doi: 10.31234/osf.io/j82uc
- ManyPrimates, Altschul, D. M., Beran, M. J., Bohn, M., Call, J., DeTroy, S., et al. (2019). Establishing an infrastructure for collaboration in primate cognition research. *PLoS One* 14:e0223675. doi: 10.1371/journal.pone.0223675
- Martinez-Conde, S., Otero-Millan, J., and Macknik, S. L. (2013). The impact of microsaccades on vision: towards a unified theory of saccadic function. *Nat. Rev. Neurosci.* 14, 83–96. doi: 10.1038/nrn3405
- Mascalzoni, E., Regolin, L., and Vallortigara, G. (2010). Innate sensitivity for self-propelled causal agency in newly hatched chicks. *Proc. Natl. Acad. Sci. U.S.A.* 107, 4483–4485. doi: 10.1073/pnas.0908792107
- Mathis, A., Mamidanna, P., Cury, K. M., Abe, T., Murthy, V. N., Mathis, M. W., et al. (2018). DeepLabCut: markerless pose estimation of user-defined body parts with deep learning. *Nat. Neurosci.* 21, 1281–1289. doi: 10.1038/s41593-018-0209-y
- McFarland, R., Roebuck, H., Yan, Y., Majolo, B., Li, W., and Guo, K. (2013). Social interactions through the eyes of macaques and humans. *PLoS One* 8:e56437. doi: 10.1371/journal.pone.0056437
- Méary, D., Wu, L., Zhinan, L., Guo, K., and Pascalis, O. (2014). Seeing two faces together: preference formation in humans and rhesus macaques. *Anim. Cogn.* 17, 1107–1119. doi: 10.1007/s10071-014-0742-3
- Mendl, M., Laughlin, K., and Hitchcock, D. (1997). Pigs in space: spatial memory and its susceptibility to interference. *Anim. Behav.* 54, 1491–1508. doi: 10.1006/anbe.1997.0564
- Mori, M., MacDorman, K., and Kageki, N. (2012). The uncanny valley [from the field]. *IEEE Robot. Autom. Mag.* 19, 98–100. doi: 10.1109/MRA.2012.2192811
- Morton, F. B., Brosnan, S. F., Prétôt, L., Buchanan-Smith, H. M., O'Sullivan, E., Stocker, M., et al. (2016). Using photographs to study animal social cognition and behaviour: do capuchins' responses to photos reflect reality? *Behav. Processes* 124, 38–46. doi: 10.1016/j.beproc.2015.10.005
- Myowa-Yamakoshi, M., Scola, C., and Hirata, S. (2012). Humans and chimpanzees attend differently to goal-directed actions. *Nat. Commun.* 3:693. doi: 10.1038/ncomms1695
- Myowa-Yamakoshi, M., Yoshida, C., and Hirata, S. (2015). Humans but not chimpanzees vary face-scanning patterns depending on contexts during action observation. *PLoS One* 10:e0139989. doi: 10.1371/journal.pone.0139989
- Nakano, T., Tanaka, K., Endo, Y., Yamane, Y., Yamamoto, T., Nakano, Y., et al. (2010). Atypical gaze patterns in children and adults with autism spectrum disorders dissociated from developmental changes in gaze behaviour. *Proc. R. Soc. B* 277, 2935–2943. doi: 10.1098/rspb.2010.0587
- Onishi, K. H., and Baillargeon, R. (2005). Do 15-month-old infants understand false beliefs? *Science* 308, 255–258. doi: 10.1126/science.1107621
- Overduin-de Vries, A. M., Bakker, F. A. A., Spruijt, B. M., and Sterck, E. H. M. (2016). Male long-tailed macaques (*Macaca fascicularis*) understand the target of facial threat. *Am. J. Primatol.* 78, 720–730. doi: 10.1002/ajp.22536
- Paukner, A., Wooddell, L. J., Lefevre, C. E., Lonsdorf, E., and Lonsdorf, E. (2017). Do capuchin monkeys (*Sapajus apella*) prefer symmetrical face shapes? *J. Comp. Psychol.* 131:73. doi: 10.1037/com0000052
- Paul, E. S., Harding, E. J., and Mendl, M. (2005). Measuring emotional processes in animals: the utility of a cognitive approach. *Neurosci. Biobehav. Rev.* 29, 469–491. doi: 10.1016/j.neubiorev.2005.01.002
- Perez, J., and Feigenson, L. (2021). Stable individual differences in infants' responses to violations of intuitive physics. *Proc. Natl. Acad. Sci. U.S.A.* 118:e2103805118. doi: 10.1073/pnas.2103805118
- Pfefferle, D., Kazem, A. J. N., Brockhausen, R. R., Ruiz-lambides, A. V., and Widdig, A. (2014). Monkeys spontaneously discriminate their unfamiliar paternal kin under natural conditions using facial cues. *Curr. Biol.* 24, 1806–1810. doi: 10.1016/j.cub.2014.06.058
- Plimpton, E. H., Swartz, K. B., and Rosenblum, L. A. (1981). Responses of juvenile bonnet macaques to social stimuli presented through color videotapes. *Dev. Psychobiol.* 14, 109–115. doi: 10.1002/dev.420140204
- Rakotonirina, H., Kappeler, P. M., and Fichtel, C. (2018). The role of facial pattern variation for species recognition in red-fronted lemurs (*Eulemur rufifrons*). *BMC Evol. Biol.* 18:19. doi: 10.1186/s12862-018-1126-0
- Rayner, K. (2009). The 35th Sir Frederick Bartlett Lecture: eye movements and attention in reading, scene perception, and visual search. *Q. J. Exp. Psychol.* 62, 1457–1506. doi: 10.1080/17470210902816461
- Reinhardt, V. (2004). Common husbandry-related variables in biomedical research with animals. *Lab. Anim.* 38, 213–235. doi: 10.1258/002367704323133600
- Rendall, D., Rodman, P. S., and Emond, R. E. (1996). Vocal recognition of individuals and kin in free-ranging rhesus monkeys. *Anim. Behav.* 51, 1007–1015. doi: 10.1006/anbe.1996.0103
- Rogers, L. J. (2014). Asymmetry of brain and behavior in animals: its development, function, and human relevance: laterality development in animal models. *Genesis* 52, 555–571. doi: 10.1002/dvg.22741
- Rohr, C. R. V., Schaik, C. P. V., Kissling, A., and Burkart, J. M. (2015). Chimpanzees' bystander reactions to infanticide an evolutionary precursor of social norms? *Hum. Nat.* 26, 143–160. doi: 10.1007/s12110-015-9228-5
- Rubio-Fernández, P. (2019). Publication standards in infancy research: three ways to make violation-of-expectation studies more reliable. *Infant Behav. Dev.* 54, 177–188. doi: 10.1016/j.infbeh.2018.09.009
- Ryan, A. M., Murai, T., Lau, A. R., Hogrefe, C. E., McAllister, A. K., Carter, C. S., et al. (2020). New approaches to quantify social development in rhesus macaques (*Macaca mulatta*): integrating eye tracking with traditional assessments of social behavior. *Dev. Psychobiol.* 62, 950–962. doi: 10.1002/dev.22003
- Satoh, S., Tanaka, H., and Kohda, M. (2016). Facial recognition in a Discus fish (*Cichlidae*): experimental approach using digital models. *PLoS One* 11:e0154543. doi: 10.1371/journal.pone.0154543
- Schell, A., Rieck, K., Schell, K., Hammerschmidt, K., and Fischer, J. (2011). Adult but not juvenile Barbary macaques spontaneously recognize group members from pictures. *Anim. Cogn.* 14, 503–509. doi: 10.1007/s10071-011-0383-8
- Schloegl, C., Kotschal, K., and Bugnyar, T. (2007). Gaze following in common ravens, *Corvus corax*: ontogeny and habituation. *Anim. Behav.* 74, 769–778. doi: 10.1016/j.anbehav.2006.08.017
- Shepherd, S. V. (2010). Following gaze: gaze-following behavior as a window into social cognition. *Front. Integr. Neurosci.* 4:5. doi: 10.3389/fnint.2010.00005
- Shively, C. A., and Willard, S. L. (2012). Behavioral and neurobiological characteristics of social stress versus depression in nonhuman primates. *Exp. Neurol.* 233, 87–94. doi: 10.1016/j.expneurol.2011.09.026
- Siebert, R., Taubert, N., Spadacenta, S., Dicke, P. W., Giese, M. A., and Thier, P. (2020). A naturalistic dynamic monkey head avatar elicits species-typical reactions

- and overcomes the uncanny valley. *Eneuro* 7:ENEURO.0524-19.2020. doi: 10.1523/ENEURO.0524-19.2020
- Sirois, S., and Jackson, I. R. (2012). Pupil dilation and object permanence in infants. *Infancy* 17, 61–78. doi: 10.1111/j.1532-7078.2011.00096.x
- Sliwa, J., Duhamel, J.-R., Pascalis, O., and Wirth, S. (2011). Spontaneous voice-face identity matching by rhesus monkeys for familiar conspecifics and humans. *Proc. Natl. Acad. Sci. U.S.A.* 108, 1735–1740. doi: 10.1073/pnas.1008169108
- Slocombe, K. E., Kaller, T., Call, J., and Zuberbuehler, K. (2010). Chimpanzees extract social information from agonistic screams. *PLoS One* 5:e11473. doi: 10.1371/journal.pone.0114733
- Smith, A. V., Proops, L., Grounds, K., Wathan, J., and McComb, K. (2016). Functionally relevant responses to human facial expressions of emotion in the domestic horse (*Equus caballus*). *Biol. Lett.* 12:20150907. doi: 10.1098/rsbl.2015.0907
- Somppi, S., Törnqvist, H., Hänninen, L., Krause, C., and Vainio, O. (2012). Dogs do look at images: eye tracking in canine cognition research. *Anim. Cogn.* 15, 163–174. doi: 10.1007/s10071-011-0442-1
- Southgate, V., Senju, A., and Csibra, G. (2007). Action anticipation through attribution of false belief by 2 year olds. *Psychol. Sci.* 18, 587–592. doi: 10.1111/j.1467-9280.2007.01944.x
- Spelke, E. S., Katz, G., Purcell, S. E., Ehrlich, S. M., and Breinlinger, K. (1994). Early knowledge of object motion: continuity and inertia. *Cognition* 51, 131–176. doi: 10.1016/0010-0277(94)90013-2
- Tada, H., Omori, Y., Hirokawa, K., Ohira, H., and Tomonaga, M. (2013). Eye-blink behaviors in 71 species of primates. *PLoS One* 8:e66018. doi: 10.1371/journal.pone.0066018
- Tafreshi, D., Thompson, J. J., and Racine, T. P. (2014). An analysis of the conceptual foundations of the infant preferential looking paradigm. *Hum. Dev.* 57, 222–240. doi: 10.1159/000363487
- Taylor, M. A. (2020). *Autonomous eye tracking in octopus bimaculoides*. B.Sc. thesis. Hanover, NH: Dartmouth College.
- Trösch, M., Cuzol, F., Parias, C., Calandreau, L., Nowak, R., and Lansade, L. (2019). Horses categorize human emotions cross-modally based on facial expression and non-verbal vocalizations. *Animals* 9:862. doi: 10.3390/ani9110862
- Tyrrell, L. P., Butler, S. R., Yorzinski, J. L., and Fernández-Juricic, E. (2014). A novel system for bi-ocular eye-tracking in vertebrates with laterally placed eyes. *Methods Ecol. Evol.* 5, 1070–1077. doi: 10.1111/2041-210X.12249
- van Rooijen, J. (2010). Do dogs and bees possess a 'theory of mind'? *Anim. Behav.* 79, e7–e8. doi: 10.1016/j.anbehav.2009.11.016
- Voelkl, B., Vogt, L., Sena, E. S., and Würbel, H. (2018). Reproducibility of preclinical animal research improves with heterogeneity of study samples. *PLoS Biol.* 16:e2003693. doi: 10.1371/journal.pbio.2003693
- Völter, C. J., and Huber, L. (2022). Pupil size changes reveal dogs' sensitivity to motion cues. *iScience* 25:104801. doi: 10.1016/j.isci.2022.104801
- Wang, S. (2004). Young infants' reasoning about hidden objects: evidence from violation-of-expectation tasks with test trials only. *Cognition* 93, 167–198. doi: 10.1016/j.cognition.2003.09.012
- Wass, S. V. (2014). Comparing methods for measuring peak look duration: are individual differences observed on screen-based tasks also found in more ecologically valid contexts? *Infant Behav. Dev.* 37, 315–325. doi: 10.1016/j.infbeh.2014.04.007
- Wathan, J., Proops, L., Grounds, K., and McComb, K. (2016). Horses discriminate between facial expressions of conspecifics. *Sci. Rep.* 6, 1–11. doi: 10.1038/srep38322
- Webb, A., Knott, A., and Macaskill, M. R. (2009). Eye movements during transitive action observation have sequential structure. *Acta Psychol. (Amst.)* 133, 51–56. doi: 10.1016/j.actpsy.2009.09.001
- Westbrook, A., and Braver, T. S. (2016). Dopamine does double duty in motivating cognitive effort. *Neuron* 89, 695–710. doi: 10.1016/j.neuron.2015.12.029
- Wilkinson, A., Mandl, I., Bugnyar, T., and Huber, L. (2010). Gaze following in the red-footed tortoise (*Geochelone carbonaria*). *Anim. Cogn.* 13, 765–769. doi: 10.1007/s10071-010-0320-2
- Wilson, V. A. D., Kade, C., and Fischer, J. (2021). Testing the relationship between looking time and choice preference in long-tailed macaques. *Anim. Behav. Cogn.* 8, 351–375. doi: 10.26451/abc.08.03.2021
- Wilson, V. A. D., Kade, C., Moeller, S., Treue, S., Kagan, I., and Fischer, J. (2020). Macaque gaze responses to the Primatar: a virtual macaque head for social cognition research. *Front. Psychol.* 11:1645. doi: 10.3389/fpsyg.2020.1645
- Winsor, A. M., Pagoti, G. F., Daye, D. J., Cheries, E. W., Cave, K. R., and Jakob, E. M. (2021). What gaze direction can tell us about cognitive processes in invertebrates. *Biochem. Biophys. Res. Commun.* 564, 43–54. doi: 10.1016/j.bbrc.2020.12.001
- Winters, S., Dubuc, C., and Higham, J. P. (2015). Perspectives: the looking time experimental paradigm in studies of animal visual perception and cognition. *Ethology* 121, 625–640. doi: 10.1111/eth.12378
- Witham, C. L. (2018). Automated face recognition of rhesus macaques. *J. Neurosci. Methods* 300, 157–165. doi: 10.1016/j.jneumeth.2017.07.020
- Würbel, H. (2000). Behaviour and the standardization fallacy. *Nat. Genet.* 26:263. doi: 10.1038/81541
- Zeiträg, C., Jensen, T. R., and Osvath, M. (2022). Gaze following: a socio-cognitive skill rooted in deep time. *Front. Psychol.* 13:950935. doi: 10.3389/fpsyg.2022.950935