

# Friend or foe? Using eye-tracking technology to investigate the visual discrimination ability of giant pandas

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## Abstract

The role that visual discriminative ability plays among giant pandas in social communication and individual discrimination has received less attention than olfactory and auditory modalities. Here, we used an eye-tracker technology to investigate pupil fixation patterns for 8 captive male giant pandas *Ailuropoda melanoleuca*. We paired images ( $N = 26$ ) of conspecifics against: 1) sympatric predators (gray wolves and tigers), and non-threatening sympatric species (golden pheasant, golden snub-nosed monkey, takin, and red panda), 2) conspecifics with atypical fur coloration (albino and brown), and 3) zookeepers/non-zookeepers wearing either work uniform or plain clothing. For each session, we tracked the panda's pupil movements and measured pupil first fixation point (FFP), fixation latency, total fixation count (TFC), and duration (TFD) of attention to each image. Overall, pandas exhibited similar attention (FFPs and TFCs) to images of predators and non-threatening sympatric species. Images of golden pheasant, snub-nosed monkey, and tiger received less attention (TFD) than images of conspecifics, whereas images of takin and red panda received more attention, suggesting a greater alertness to habitat or food competitors than to potential predators. Pandas' TFCs were greater for images of black-white conspecifics than for albino or brown phenotypes, implying that familiar color elicited more interest. Pandas reacted differently to images of men versus women. For images of women only, pandas gave more attention (TFC) to familiar combinations (uniformed zookeepers and plain-clothed non-zookeepers), consistent with the familiarity hypothesis. That pandas can use visual perception to discriminate intra-specifically and inter-specifically, including details of human appearance, has applications for panda conservation and captive husbandry.

**Key words:** eye movement tracker, giant panda, images, total fixation duration, total pupil fixation count, visual discrimination.

In nature, no species exists in isolation, and thus the ability to discriminate, recognize and classify other sympatric organisms into positive/useful, neutral/non-threatening, or negative/potentially harmful is fundamental to the survival and fitness of all animals (Lind and Cresswell 2005). For instance, among conspecifics, social partners or potential mates would be classed as “positive/useful,” whereas competitors for food or mating opportunities, or even threats from human activity, would be classed as potentially negative/harmful. Similarly, “useful” and thus beneficial interactions with non-conspecifics would include distinguishing potential prey species or inter-specific collaborators, such as American badgers *Taxidea taxus* hunting mutualistically with coyotes *Canis latrans* (Minta et al. 1992). Sympatric non-prey species that occupy different ecological niches and thus do not compete for food/habitat would present neutral/non-threatening interactions, whereas contact with predators or potentially aggressive competitors would pose a risk of “threatening/

harmful/dangerous” interactions, best avoided. Building on these powers of discrimination, many mammals have the cognitive ability to understand social relationships among different conspecific individuals and predict their behavior in context (see reviews by Carlson et al. 2020; Seyfarth and Cheney 2015; Wyman et al. 2022, and studies on bottlenose dolphins *Tursiops truncatus* by Janik et al. 2006 and Mustelidae by Newman and Buesching 2018). Mammals use a mixture of sensory modalities for these types of discrimination, including visual, auditory and chemosensory signals or cues (Parr and de Waal 1999; Kavaliers et al. 2005; Johnston 2008), although diurnal mammals often have a visual bias.

Among mammals, targeted research into the cognitive ability to discriminate visually is, however, limited by the fact that not all species can interpret a 2-dimensional (2D) image as a meaningful representation of a real 3-dimensional object (Bovet and Vauclair 2000; Parron et al. 2008; Truppa et al. 2009). For instance, while Truppa et al. (2009) demonstrated

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that captive capuchin monkeys *Cebus apella* can establish a correspondence between a pictorial representation and a real object, Parron et al. (2008) found that naïve baboons *Papio anubis* and gorillas *Gorilla gorilla* did not process the pictures as representations, but rather mistook the image for a real piece of banana and ate it. In contrast, chimpanzees *Pan troglodytes* did not eat the image but appeared to recognize the food item depicted as a referent. Captive capuchin monkeys (Pokorny and de Waal 2009), domestic cattle (*Bos taurus*, Coulon et al. 2011), and domestic dogs (*Canis familiaris*, Somppi et al. 2014) can distinguish between facial images of familiar and novel conspecifics. Japanese macaques *Macaca fuscata* can even distinguish between male and female macaques from full-body images, but show more interest in images of novel sex than previously familiarized sex (Koba and Izumi 2008). This ability to discriminate from 2D facial images extends to distinguishing heterospecific congeners in wild red-fronted lemurs *Eulemur rufifrons*, which correlates negatively with genetic distance (Rakotonirina et al. 2018). Captive chimpanzees *Pan troglodytes* can detect strange/abnormal body parts imposed on images of conspecifics (Gao et al. 2022), and wild chimpanzees *P. t. schweinfurthii* can learn new sign-language gestures from pictorial images (Roberts and Roberts 2019). Bellegarde et al. (2017) even proposed that sheep *Ovis aries* can decipher the emotional state of conspecifics from pictorial images.

Studies have also demonstrated that some domesticated animals can discriminate human features from pictorial images. For instance, riding horses (domesticated *Equus caballus*) can discriminate familiar and novel human facial images, including distinguishing identical twins (Stone 2010). Similarly, domestic dogs can discriminate familiar from novel images of humans, even if images are inverted (Somppi et al. 2014). Pigs (*Sus scrofa domestica*, Wondrak et al. 2018) and domestic horses (Nakamura et al. 2018) can even distinguish and interpret human facial expression from pictures. This ability can be important for domesticated animals, wild animals in captivity, and even animals living in the wild, if they are hunted or persecuted; for instance, wild wapiti *Cervus canadensis* can discriminate the orange vests worn by hunters (Scott 1981).

To date, studies investigating the ability of large solitary carnivores to discriminate visually, especially based on 2D pictorial images, have focused predominantly on the Ursidae, such as American black bears (*Ursus americanus*; e.g., Vonk et al. 2021), sloth bears (*Melurus ursinus*; e.g., Tabellarario et al. 2020), and sun bears (*Helarctos malayanus*; e.g., Perdue 2016). Previous studies in captivity have shown that another ursid, the giant panda *Ailuropoda melanoleuca*, can innately discriminate the urine of predator versus non-predator (Du et al. 2012), and in this study we explore the giant pandas' (hereafter "panda") visual discrimination ability, relating to conspecifics, hetero-specifics, and those humans they encounter in a captive setting. Pandas are solitary, cathemeral, and feed almost exclusively on bamboo (Schaller et al. 1985). Wild pandas are endemic only to China, where they are distributed within forests and bamboo stands across over 6 fragmented mountainous areas in Sichuan, Shaanxi, and Gansu province (State Forestry and Grassland Administration P. R. China 2021). The aposematic black and white wild-phenotype panda coloration presents a distinctive visual cue (Newman et al. 2005), suggesting that they may utilize vision as a key perceptual modality, alongside interpreting chemosensory cues. For instance, when wild pandas scent-mark they often also

scratch the bark of trees, leaving a visual signal (Schaller et al. 1985). Vision may aid pandas when discriminating conspecifics at a distance, detecting salient black-white fur coloration with a distinct black eye mask, as well as mutant fur color phenotypes, where brown pandas are reported frequently in the Qinling Mountains, Shaanxi Province (Editorial 1991) and a wild albino panda was recently discovered in the Wolong Nature Reserve, Sichuan Province (Chang 2019). Vision may also assist pandas to discern sympatric species (Li et al. 2020) and "ghosts of recent predators past" (Silliman et al. 2018), particularly those that could pose a threat to them or their vulnerable altricial neonates (Schaller et al. 1985), such as south China tigers *Panthera tigris amoyensis*, leopards *P. pardus*, snow leopards *Uncia uncia*, leopard cats *Prionailurus bengalensis*, Asian golden cats *Catopuma temminckii*, gray wolves *Canis lupus*, dholes *Cuon alpinus*, red foxes *Vulpes vulpes* and yellow-throated martens *Martes flavigula*. Pandas occur alongside a guild of 54 other non-threatening mammal species, among which 5 are competitors for food, dens (Lai et al. 2020), and spatial range (takins *Budorcas taxicolor*, Asiatic black bears *Ursus thibetanus*, wild boar *Sus scrofa*, red pandas *Ailurus fulgens* and Chinese bamboo rats *Rhizomys sinensis*) (State Forestry and Grassland Administration P. R. China 2021). In addition, the Asiatic black bear and wild boar can pose a threat to neonatal and juvenile pandas, if these are left unattended.

Better understanding the ability of pandas to discriminate humans from other animals visually is important because this has likely been advantageous during their recent evolution, due to encroachment on panda habitat by villagers, agriculture, and livestock. This severely impacted their habitat and caused a catastrophic decline in their numbers in the latter part of the 20th Century, so much so that concerted conservation efforts in China since 1989 have been necessary to recover giant pandas from the brink of extinction. (Hu 1990; Hull et al. 2014; Wang et al. 2015). Support for the ability of pandas to recognize and discriminate humans comes from a study by Li et al. (2017) who demonstrated that captive pandas are actually capable of distinguishing human emotions as portrayed in pictures depicting different facial expressions.

The underlying visual acuity of pandas is fundamental to the design and interpretation of any experiment intending to test their powers of perception. A study on captive pandas found that they have acute eyesight and can distinguish black stripes as narrow 0.46 mm on a white background from a distance of 0.5 m, but not 0.34 mm wide stripes (Lin et al. 2018). With training, captive pandas can learn to discriminate panda-like eye-mask patterns from photoshopped images, even when manipulated into different shapes (Dungl et al. 2008). Pandas can also differentiate between red and green-colored printed rectangles (Kelling et al. 2006), suggesting that they have well-developed color vision, exceeding that previously attributed to *Ursus* spp. (Pelton et al. 1976).

Given this evidence for the potential importance of visual perception in pandas, it is important that any empirical investigation is conducted using sensitive instruments, while applying an objective approach to reduce possible observer bias/errors when classifying the animal's behavioral responses. To these ends, in this study, we used a widely applied ophthalmology instrument, namely the "eye tracker" (see Kano and Tomonaga 2009; Hopper et al. 2021; Lewis and Krupenye 2022), to investigate differences in gaze direction and pupil fixation patterns (measured as time spent looking at each

image) among captive giant pandas presented simultaneously with paired color images. Such 2-choice tests are a commonly used procedure for investigating discriminative ability in animal behavior and psychology studies (Boelens 2002), and are interpreted from differences in either the frequency or the time duration the animal spends investigating 2 stimuli. Our experiments were designed to test, the ability of pandas to distinguish: 1) a predator or a non-threatening species from a black-white panda; 2) a conspecific with the typical black-white fur coloration from an albino or brown conspecifics; 3) a male or female (separately) zookeeper with which the panda was acquainted (i.e., known to the panda, but not involved in that panda's primary care) from a male or female non-zookeeper dressed in work uniform/plain clothing. This third contrast was intended to ascertain if an out of context presentation of an image of a person (zookeeper in plain clothing or non-zookeeper in uniform) would be salient and catch the attention of the panda, or whether their attention would be drawn more to a familiar context image (zookeeper in uniform or non-zookeeper in plain clothes). We then discuss how pandas' visual discrimination ability may affect their social behavior and mate choice, placing our findings in the broader paradigm of animal cognition. We also consider the practical application of our findings to both *in situ* and *ex situ* panda conservation strategies.

## Material and Methods

### Subjects and housing conditions

These experiments were conducted at the China Conservation and Research Center for the Giant Panda (CCRCGP), Gengda Base, Sichuan Province, from May to June, 2019. All adult female pandas kept at this base were either involved in the annual breeding program or nursing infant pandas, therefore we used 8 adult male pandas as subjects (Supplementary materials, Supplementary Table 1). All subjects were kept individually in enclosures comprising an indoor pen (5.8 × 2.3 m) and an outdoor enclosure (5.8 × 13.0 m), complete with a water fountain and grass. All parts of the enclosures were freely accessible to each panda at all times. The indoor pens and outdoor enclosures were cleaned each morning at around 8:00 AM by zookeepers. All pandas were fed twice daily with fresh bamboo, bamboo shoots, steamed bread made from maize, powdered bamboo and nutritional supplements/vitamins, apples, carrots and honey by zookeepers (Liu et al. 2013). Note, images of these specific zookeepers were not used in our subsequent experimental sessions, so that subject pandas would not associate images with the provision of food or care. None of the animals had been used in any visual stimuli tests prior to this study, and all were healthy during our tests. These tests had no negative effects on the health or welfare on these pandas.

### Apparatus and validation of eye-tracker methodology

We used a SMI RED250 Eye Tracker (SMI, Berlin, Germany), commonly used in ophthalmology to track human pupil movements (Poiroux et al. 2015; Gantz and Caspi 2020). This device samples at a frequency set at 120 Hz, with a resolution of 1280 × 1024 pixels. Based on the protocol described in Park et al. (2019) in a similar study on domestic dogs, we first conducted a pilot phase using a female panda at Beijing Zoo to ensure that the eye tracker could track panda eye

movements accurately. We acclimated this female to the eye tracker and associated experimental apparatus by placing this equipment in a small, fenced enclosure within her indoor room with access to this area by the experimenter from outside of her pen, but without constraining or affecting her activity (Supplementary Figure S1).

To calibrate the eye tracker during this pilot phase, we followed the procedure established for humans, first calibrating the instrument, then validating these results (Wang et al. 2016). To do this, we first used an operant conditioning procedure to train the panda to look at a 54-inch (137 cm) flat LED screen 70 cm back from the fenced enclosure housing the apparatus. A zookeeper called the panda's name from behind the LED screen and directed her attention to the screen (note: these pandas are trained to follow commands). A second person (author XQH) adjusted the angle of the eye tracker to track the panda's eye movement and calibrated and validated the eye tracker set-up using 4-point method (Supplementary Figure S2). To attract the panda's attention, we replaced the moving cursor on the screen with the moving image of a red apple (i.e., a favorite food). The apple occupied approximately 1/24 of the screen and was presented on a gray background. The panda was rewarded with a piece of apple or a bamboo shoot whenever she successfully participated in the task (i.e., focused her pupils on the apple image resulting in the eye tracker generating a dot that aligned on the picture of the apple on the LED screen). After 3–5 training repetitions, the panda understood the task and easily and voluntarily followed instructions, focusing its attention on the pictures displayed on the LED screen. Next, the operator operated a laptop computer connected to the LED screen, continuously playing back 2 parallel images (via PowerPoint), with the screen divided vertically in equal-sized left and right panels. Each image pair was presented randomly to the subject panda for 3–5 s. To reduce the effects of image pair fatigue, a grey background image was presented to the subject between image pairs as a 2–4 s interlude.

To examine the panda's primary attention to either 1 of the 2 images during this validation, we did not use the area/region of interest approach (as typically used in human studies), but rather the points of interest on the image, as determined from pupil fixation prediction. We did so because we had to use a swift and efficient approach, rather than a totally comprehensive one, for the sake of animal welfare and experimenter safety. After using a female panda at Beijing Zoo in our pilot study to develop the most suitable protocol, we conducted our full regimen of experimental tests with the 8 captive males at the CCRCGP.

### Test images

We used a digital camera (Canon 5D Mark II, Canon, Japan) to take color pictures (resolution 4032 × 2272 pixels) of male and female zookeepers (randomly selected from zookeepers who were caring other pandas than our 8 subjects, that is, with whom the subject pandas would be sufficiently acquainted to recognize as zookeepers, but without associating these personnel with food or care) and non-zookeepers (randomly selected from among D Liu's lab graduate students). The pictures depicted these people from above the waist, with facial expressions ranging from neutral to cheerful, as would be typical for people working around these pandas. All other animal images used were downloaded from Baidu ([www.baidu.com](http://www.baidu.com)) with a resolution of no less



than  $800 \times 800$  pixels. The total area of the image in each tested category (animals or people) was no less than 75% of the whole area of the total picture. The paired images of zookeepers and non-zookeepers used the same background, the animals (conspecifics, and sympatric species) used the natural environment in which they were photographed as background. We presented these image pairs in 3 groups: *Group 1*: pairing the same picture of an unfamiliar black-white panda with either a predator (gray wolf; tiger) or a non-threatening species (golden pheasant *Chrysolophus pictus*, golden snub-nosed monkey *Rhinopithecus roxellana*, takin, red panda) (Supplementary Figure S3); *Group 2*: pairing the same image of a black-white colored panda with either an albino panda or a brown panda (Supplementary Figure S4); *Group 3*: pairing images of acquainted male ( $N = 2$ ) or female ( $N = 2$ ) zookeepers versus non-zookeepers wearing either work uniform ( $N = 2$ ) or plain clothing ( $N = 2$ ) (Supplementary Figure S5). For full details of image pairings see Supplementary Table 2. We acknowledge that it is possible that subject pandas were recognizing specific features of those pandas or people depicted in our limited set of images, rather than responding to those traits we intended to examine, per se; however, our sessions had to be expedient, and not involve replicate images, to avoid stressing participating subject pandas.

### Test procedure

All tests were carried out in the corridor ( $12.7 \times 2.7 \times 3.6$  m) of the breeding center at CCRCP to provide a familiar environment. Because the eye tracker uses an infrared ray to track the pupil, we covered the glass roof of the corridor with opaque sheets and hung curtains at each end of the corridor to exclude sunlight and to dim the light intensity in the test environment to approximately 19.4 lux.

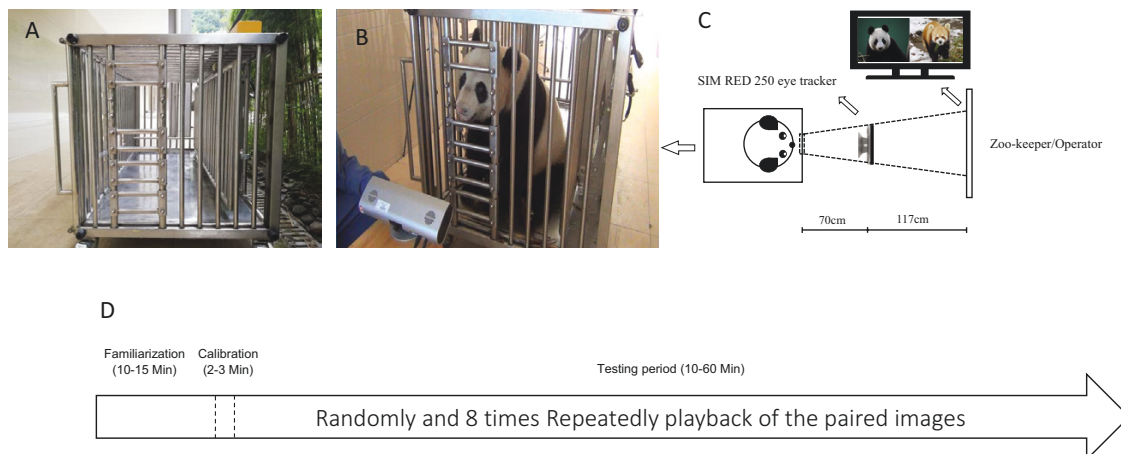
We used a metal bar cage ( $2.05 \times 0.8 \times 1.0$  m, Figure 1A) to contain the subject panda, as commonly used for translocating pandas between different enclosures, breeding enclosures, or to the hospital room for veterinary exams. This cage had an unobstructed square window ( $20 \times 20$  cm) on 1 side through which the panda (Figure 1B) could look at a 55-inch (140 cm) LED screen (HIKVISION DS-D5055FC,

HIKVISION, Hangzhou, China), which was placed parallel to the cage at a distance of 1.87 m, which we established was optimal in our pilot phase (Figure 1C). Before the start of each experiment, the panda was directed to enter the cage and given 10–15 min to settle down. These pandas are well-trained to follow vocal commands, using small food rewards, and could be directed to assume a half-sitting posture and to put their faces close to the small window of the cage, looking at the screen (Figure 1B). Whenever the panda followed the zookeeper's instructions and looked attentively through the window at the screen, its pupil movements were automatically tracked by the eye movement detector (Figure 1C).

To initiate each experimental session, a keeper behind the TV screen (with only their legs visible to the panda) used a small food incentive (e.g., a piece of apple) to induce the panda to center its eyes on the screen (Figure 1B). This zookeeper was blind to the content and combinations of the images on the screen. A second person (Author XQH) adjusted the angle of the eye tracker according to the pilot phase calibration (Supplementary Figure S1). Each trial began when deviation from calibration levels along both the *X* and *Y* axes was less than  $0.5^\circ$ .

Image pairs were then presented randomly to the subject panda in 3 separate groups to test each of 1) predator and sympatric non-threatening species discrimination (12 pairs), 2) conspecific coloration discrimination (6 pairs), and 3) zookeeper discrimination (8 pairs) (Figure 1D, Supplementary Table 2 and Supplementary Figures S3–5). At least 8 replicate sessions were conducted per subject panda, each on a different day. The procedure followed was the same as in the pilot study.

If a panda lost interest in the images or became frustrated, the zookeeper would placate it with either a piece of apple or a drop of honey, and then the testing was resumed. Whenever this happened, the session had to be recalibrated. If a panda was persistently uncooperative the experiment was suspended in the interest of the panda's welfare, and the subject panda was substituted with a different individual. Typically, only 2 to 3 pandas could be tested each day. It took a total of 132 h over 25 days to complete all of this testing.



**Figure 1.** (A) The empty cage housing the panda (note the small window on the front side of the cage) and (B) the panda looked at the screen through the small window from a half-sitting posture (note the left lower corner shows the eye tracker in front of the cage). (C) A schematic figure showing the position of the panda cage, eye tracker and the LED TV. (D) A schematic figure depicting the testing procedure.

## Data collection

We used the following parameters collected by the SMI RED250 eye tracker

### First focus of visual attention

#### a) First fixation point:

The location of the pupil's first fixation point (FFP) on either 1 of the 2 juxtaposed images per session was recorded as a metric of which image first caught the panda's attention. We defined the FFP according to whether it occurred on the left or the right image between the pair presented; attention to any part of the picture other than the target image (e.g., the image background) was disregarded. For each subject, the relative ratio of initial FFP on either the right or left image was used for further analysis. This relative ratio was calculated as the total number of the first attention events given to the right (or left) image panel per session of all sessions divided by the total number of sessions repeated for each group (predator/conspicific/zookeeper) and individual subject.

#### b) Latency:

Latency was defined as the amount of time (in microseconds) elapsing between image pair presentation to the panda and the fixation of its pupil's gaze on an image. We standardized latency in each trail by dividing it by the total session duration. Each panda was shown the same group of images 2–7 times depending on the panda's temperament and performance, and then mean latency for each image group, per panda, was used in all subsequent analyses.

### Continuous attention focus

#### a) Total fixation counts:

The total number of fixations on each image recorded during the presentation of each image pair was recorded. Attention focused on any part of the picture other than the target image was excluded from analysis.

#### b) Total fixation duration:

This was defined as the total fixation time a panda focused on either the left or the right image in each session. According to [Hu et al. \(2013\)](#), and considering the gaze characteristics (such as duration of fixation) of the giant panda, the minimum duration of fixation was set at 50 ms, and all events < 50 ms were considered part of a saccade (i.e., the quick, simultaneous movement of both eyes between 2 or more phases of fixation in the same direction) and thus excluded from subsequent analysis.

## Statistics

We analyzed these FFP, relative latency of FFP, total fixation count (TFC) and total fixation duration (TFD) parameters for each group of test images (1–3). FFP was analyzed using a binomial test. Relative latency of FFP per session for each panda was arcsine transformed as the response variable, with image group as the fixed effect, and each panda's identity and session repetition as random factors. A GLMM with gamma distribution was then used to examine for differences in the latency of FFP for the paired images. For TFC and TFD, we again used GLMMs to analyze differences between paired images from the same group (predators/conspicifics/zookeepers), with the absolute difference in TFCs or TFD on the 2 target images of each session and the panda's identity and

session repetition as random factors, with image group as the fixed effect. We applied a Negative-Binomial Regression model to TFC and Custom Normal analyses to TFD.

All statistical analyses were conducted in SPSS 22.0 (IBM Incorporation, Armonk, USA), and all tests were 2-tailed. Alpha level was set at 0.05.

## Results

### Do pandas show different responses to conspecific images compared to predators or other non-threatening animal species?

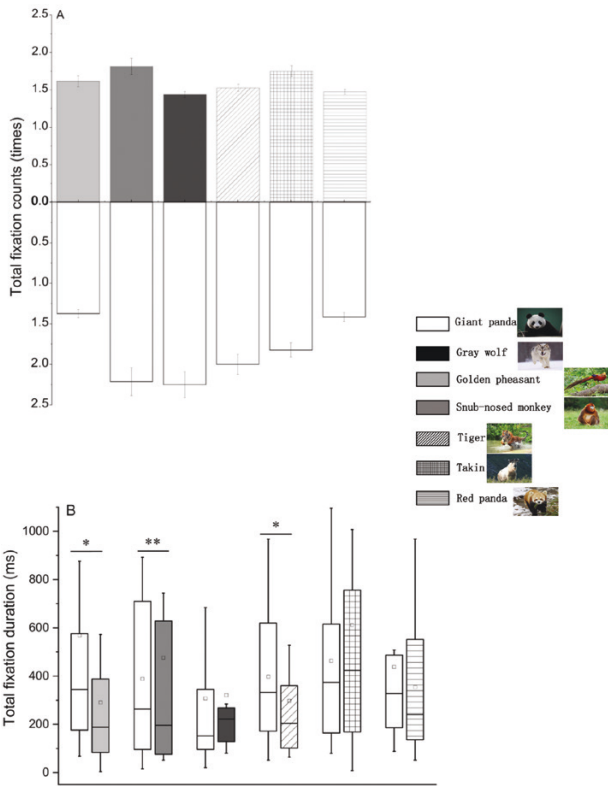
Overall, in terms of FFPs and TFCs, pandas did not exhibit different levels of attention to images of predators or sympatric non-threatening species when presented paired with images of conspecifics (Binominal test, [Figure 2A](#) and [Supplementary Figure S6](#)). Their TFDs spent on conspecific images was, however, significantly longer when paired against images of golden pheasant, snub-nosed monkey and tiger (GLMM,  $P = 0.048$ ,  $0.002$ , and  $0.013$ , respectively); conversely, their TFD on images of takin and red panda was longer than their TFD on conspecifics (GLMM, both,  $P > 0.05$ , [Figure 2B](#)). There was no significant difference in FFP latencies when viewing images of conspecifics paired with images of predators or sympatric non-threatening species (GLMM, all  $P > 0.05$ , [Supplementary Figure S7](#)).

### Do pandas show different responses to conspecifics with different fur coloration?

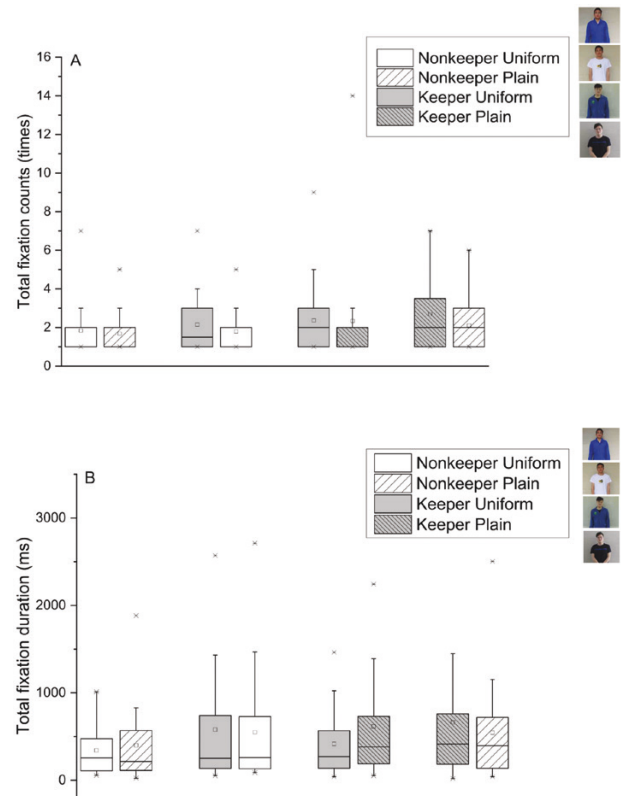
Pandas' TFCs were greater for images of black-white colored conspecifics than for albino or brown-colored pandas (Binomial test, both  $P = 0.000$ ). There were no significant differences in TFCs between images of albino and brown-colored conspecifics (GLMM,  $P = 0.82$ , [Figure 3A](#)), although they spent significantly more time inspecting images of albinos versus brown pandas (GLMM,  $P = 0.023$ , [Figure 3B](#)). No significant difference in FFPs (Binominal test, all  $P > 0.05$ ; [Supplementary Figure S8](#)) or FFP latencies (GLMM, all  $P > 0.05$ , [Supplementary Figure S9](#)) were found in response to any of the 3 fur color image combinations.

### Do pandas show different responses to acquainted zookeepers versus non-zookeepers in work uniform or plain clothing?

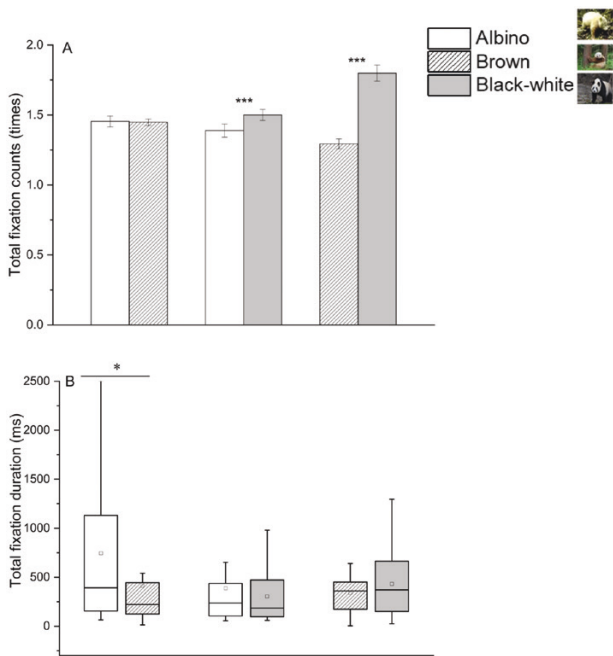
Overall, pandas showed no significant differences in their TFC and TFD to any image combinations of acquainted zookeepers and unfamiliar non-zookeepers in plain clothing versus work uniform when these images were of men (GLMM, both  $P > 0.05$ , [Figure 4A, B](#)). Interestingly, however, when these images depicted women, pandas gave significantly more attention, in terms of TFC, to images of acquainted zookeepers versus non-zookeepers when both wore work uniform (GLMM,  $P = 0.019$ , [Figure 4A](#)). Conversely, they gave more attention, in terms of TFC, to images of female non-zookeepers versus acquainted zookeepers when both wore plain clothing (GLMM,  $P = 0.004$ , [Figure 4A](#)), although they spent significantly more time looking at images of female acquainted zookeepers than non-zookeepers when both wore plain clothing (GLMM,  $P = 0.043$ , [Figure 4B](#)), and also spent significantly more time inspecting images of female non-zookeepers in work uniform than time on non-zookeepers in plain clothing (GLMM,  $P = 0.002$ , [Figure 4B](#)). Overall, however, there was no significant difference in FFP for any



**Figure 2.** Relative total fixation count responses (A) and relative total fixation duration responses (B) to different image combinations of black–white conspecifics, albino and brown conspecifics. \*  $P < 0.05$ , \*\*\*  $P < 0.001$ .



**Figure 4.** Total fixation count responses (A) and total fixation duration responses (B) to different image combinations of female, acquainted zookeepers versus non-zookeepers in work uniforms versus plain clothing. \*  $P < 0.05$ , \*\*  $P < 0.01$ . Note: the fourth box on panel a indicates non-zookeeper in work uniform.



**Figure 3.** Total fixation count responses (A) and total fixation duration responses (B) to different image combinations of male, acquainted zookeepers versus non-zookeepers in work uniforms versus plain clothing.

of the image combinations of (male/female) acquainted zookeepers in work uniforms or plain clothing (Binominal test,

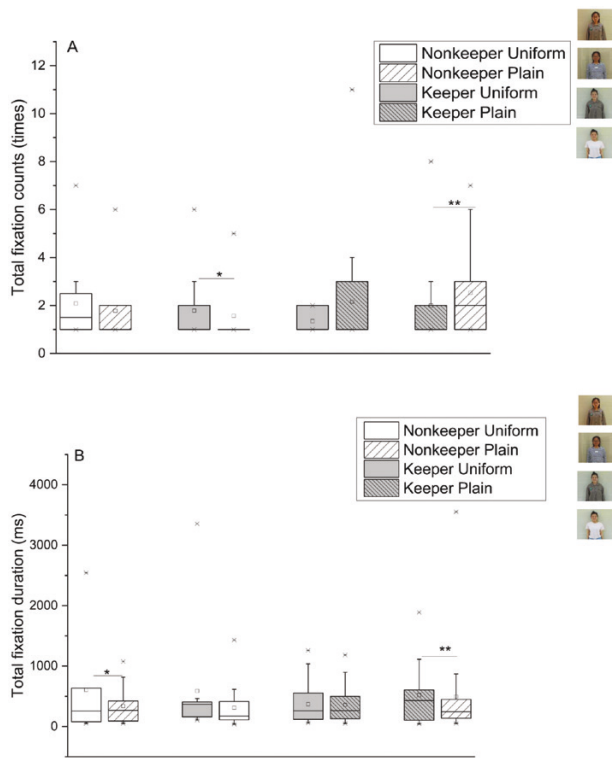
both  $P > 0.05$ , [Supplementary Figure S10](#)). Further analyses of FFP latency revealed only that pandas took less time to fixate on images of male acquainted zookeepers contrasted with non-zookeepers when they were both in plain clothing (GLMM,  $P = 0.026$ ); no significant differences were found for any other image combinations (GLMM, all  $P > 0.05$ , [Supplementary Figure S11](#)).

### Discussion

Few studies have used 2D images and eye movement tracking technology to test the visual discrimination ability (specifically, spontaneous viewing preferences, measured as FFP) of large, captive non-domesticated mammals, (but see [Hopper et al. 2021](#)), and, to the best of our knowledge, ours is the first study of this kind on giant pandas. We found that pandas showed significantly more interest, in terms of TFD, in images of conspecifics than in those of other sympatric species, including a potential predator. They also showed more interest, in term of TFC, in images of conspecifics with typical black-white fur color than in those of pandas with albino or brown fur; although, in terms of TFD, they were more interested in images of albinos when paired with brown fur color individuals. Pandas reacted differently to images of men versus women, which, in the case of women only, was moderated by the clothing they wore (plain vs. uniform).

Previous studies have found that American black bears ([Johnson-Ulrich et al. 2016](#)) and sloth bears ([Tabellario et al. 2020](#)) are capable of abstract discrimination from 2D





**Figure 5.** Total fixation count responses (A) and total fixation duration responses (B) to different image combinations of conspecific, sympatric non-threatening species, and predators. \*  $P < 0.05$ , \*\*  $P < 0.01$ .

pictures, as a transference from their responses to the real objects/animals. The giant panda has a similar brain structure to that of other Ursidae (Mettler and Goss 1946), but with a relatively greater progression index (a measure of the degree to which the size of a particular brain structure in a given mammal diverges from the prediction for a hypothetical insectivore of its same body size, Stephan et al. 1970), neocortex ratio (Kamiya and Pirlot 1988) and corpus striatum (Xie et al. 1984), which typically implies superior cognitive abilities (Lefebvre et al. 2004; Stankowich and Romero 2017). Certainly, in urine provisioning experiments, pandas exhibit a greater response to the urine of carnivores such as snow leopards, leopards and dholes, than to other non-threatening conspecific species, even if they were not familiar with these respective species (Du et al. 2012). A study by Zheng (2016) demonstrated that wild pandas will avoid leopard urine placed along a trail, but do not avoid the urine of conspecifics or of Chinese goral *Naemorhedus caudatus*. Congruent with this innate olfactory ability (Du et al. 2012), from TFD responses, we found that pandas were clearly able to visually discriminate 2D images of conspecifics, potential predators, and non-threatening sympatric species, and we infer from this that they would modify their behavioral responses accordingly if they observed these animals in reality. This visual ability is consistent with findings for domestic dogs (Somppi et al. 2014), cattle (Coulon et al. 2011), and wild red-fronted lemurs (*Eulemus rufifrons*, Rakotonirina et al. 2018).

More specifically, we found that the pandas' TFCs were not significantly different for potentially threatening species (i.e., predators or food competitors) contrasted against non-threatening/neutral species, when compared with their TFCs in response to conspecifics (Figure 8A). Nevertheless,

they did spend significantly more time (TFC) on images of conspecifics compared to golden pheasants, golden snub-nosed monkeys, and tigers (Figure 8B). Due to their large body size, potential ferocity, and activity patterns (Schaller et al. 1985; Wei et al. 1989), adult pandas are rarely vulnerable to predation in the wild, however, their neonates and infants are. Mothers provide fastidious care for their offspring of up to 18 months old (Schaller et al. 1985; Lü et al. 1994), and even fast for 2-weeks post-partum, so as not to leave their infant to go foraging (Zhu et al. 2001); even thereafter, they leave their offspring only briefly (Zhu et al. 2001). As cubs mature, mothers will “park” them in tree-tops during their foraging forays and call them back down to the ground upon their return (D. Liu, unpublished data). This could potentially result in a selection pressure for mothers to be able to discriminate and respond to immediate threats to their cubs using vision (Schaller et al. 1985). Relevant here is that in our experiment images were presented only to males, and future work will compare if (parous) females respond to images differently. Physiologically, however, the pandas' visual acuity of c. 0.46 mm would result in near-sightedness (myopia) in humans (Lin et al. 2018). This implies that their ability to detect and discriminate real predators at a distance would be limited, and that the short range presentation of 2D images may not be representative. Furthermore, moving objects, such as real predators, attract an animal's attention more easily than stationary ones (Tutsumi et al. 2012; Volter and Huber 2022), and thus the presentation of static images may lack the motion cues that facilitate predator discrimination. Future experiments using video clips rather than stills (as in our study) would be needed to test this hypothesis.

Pandas in our experiments not only showed interest in images of predators but also in sympatric intra-niche competitors (such as takin and red pandas), commensurate to their degree of niche overlap. This may indicate that pandas are aware of, and alert to, the risk of competition for food and habitat. In support of this, a study in Liangshan Prefecture, Sichuan Province, has shown that the habitat breadth utilized by the red panda completely encompasses the habitat breadth of the giant panda (Qi et al. 2009). In winter, both giant- and red- pandas feed on the same bamboo species *Bashania faberi* in Fengtongzhai Nature Reserve, Sichuan Province (Zhang et al. 2006), consuming bamboo shoots and leaves with a trophic niche index overlap of 0.347 (Wei et al. 1999). Similarly, the high TFD response pandas made to images of takin, may relate to competition for utilizable space. Wan et al. (2005), supplemented by new data from Fang SG (personal comm.), found that the long-distance dispersal of pandas within the Tangjiahe Nature Reserve, Sichuan Province, was impeded by an increasing population of takin inside the reserve that monopolized available space, resulting in panda philopatry, leading to inbreeding. These types of competition may exert a selection pressure for pandas to be able to recognize natural competitors. All except 3 subject pandas (named Yi-Bao, Wu-Gang, and Bai-Yang) in our study were captive born, and thus had never had any direct encounters with takin or red pandas, suggesting these responses may be innate.

Our result, where conspecifics with typical black-white fur coloration received more attention than albinos, which in turn received more attention than brown panda images, suggests that fur color plays a role in discriminating conspecifics. This discrimination bias is consistent with the findings of Dungl et al. (2008), who proposed that giant pandas

may be capable of using fur and the facial mask patterns for individual recognition, social communication, and perhaps, mate choice (see also [Caro et al. 2017](#)). There is even evidence that eye patch symmetry might provide an individual fitness indicator ([Swaddle 1996](#)). [Newman et al. \(2005\)](#) posited that salient, aposematic panda fur coloration may have evolved in various mesocarnivore species advertise to potential predators that these are fierce and not to be mistaken for prey species, compromising evolutionary selection for crypsis. Other visual functions in social communication may then have arisen secondarily to this. In comparison, the importance of urinary semio-chemical cues has been well-established for intra-specific communication among pandas (e.g., [Hagey and MacDonald 2003](#); [White et al. 2004](#); [Liu et al. 2008](#); [Nie et al. 2012](#)), and for the individual recognition of conspecifics ([Gilad et al. 2016](#)). It is thus likely that pandas combine visual and olfactory cues, along with auditory cues, to achieve both intra- and inter-specific communication ([Proops et al. 2009](#); [Ratcliffe et al. 2016](#); [Li 2019](#)). This infers that it is important to better understand the social and evolutionary basis for the high occurrence of brown pandas in the Qinling Mountains ([Editorial 1991](#)) and the rare occurrences of albino pandas at the Wolong Nature Reserve ([Chang 2019](#)). Particularly, this could have implications for mate choice, affecting both natural population dynamics and captive breeding programs ([Martin-Wintle et al. 2015, 2019](#)).

Interestingly, all pandas in our study gave more attention to female than to male (non-)zookeepers, regardless of whether they were dressed in zookeeper uniform or in plain clothing ([Figures 3 and 4](#)). The reasons for this remain unclear. These 8 study pandas were cared for primarily by 2 female and 4 male zookeepers along with male and female reserve zookeepers who substitute when primary keepers have rest days off work, and so would have no learned basis for focusing their attention on one sex over the other. Pandas checked the images of acquainted female zookeeper more than they did non-zookeepers when both were presented in work uniforms, however, the reverse was true when they were presented in plain clothing. Thus, overall, these pandas spent more time examining images of non-zookeepers in work uniforms or acquainted zookeepers in plain clothing. The work uniform of zookeepers we used in our tests is broadly used in the base and is thus familiar to subject pandas. That work uniform familiarity is important visual cue for pandas is consistent with observations by [Li et al. \(2017\)](#), and congruent with the “familiarity hypothesis” ([Johnson-Ulrich et al. 2016](#)). These results also have practical application for further improving and refining facility operational guidelines, such as minimizing staffing changes involved in panda care ([Fernandez et al. 2009](#)).

To build upon our findings, our further experiments will examine the visual responses of female pandas. We hypothesize that, reciprocally, female pandas might show greater interest in male zookeepers. This would further reinforce our emergent thesis that captive pandas may have the cognitive capacity to identify whether humans are male or female from photographs. We also concede to an imperfect execution of our study design, due to some pandas being less cooperative than others in the testing scenario. Nevertheless, and despite the risk that inconsistencies could affect results, we found no significant effect of session repetition time on visual response metrics (data not shown).

Ideally, we would conceive of a better constraint-free apparatus with which to run this eye-tracker experiment in the future.

Cognitive abilities can vary dramatically among species, and the relative importance of social and ecological challenges in shaping cognitive evolution has been the subject of a long-running and recently renewed debate ([Miller et al. 2020](#)). Our study provides a first attempt to investigate the visual discriminative abilities of giant pandas and suggests an influence of both intra- and inter-specific (including humans) perception and discrimination in shaping the evolutionary dynamics of pandas’ cognitive abilities. Through better understanding these abilities we hope that giant panda conservation strategies can be adapted to further promote coexistence in ecological communities and alleviate human-wildlife conflicts. A greater understanding of the visual ability of pandas also has applied, practical implications for individuals in captivity, such as informing enclosure design to provide behavioral enrichment for all sensory modalities, as part of best practice.

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## Ethical statement

Our experiments were carried out following the regulations of CCRCGP and adhered strictly to the Chinese Regulations and Standards for Captive Animals. The protocol was approved by the Animal Welfare and Ethics Committee of Beijing Normal University and the China Conservation and Research Center for the Giant Panda.

## Data availability

The data underlying this article will be shared on reasonable request to the corresponding author.

## Author contributions

Conceptualization: DZL, GQZ; Methodology: MDZ, LZ; Software: MT, QHX; Formal analysis: XRH, DZL; Investigation: XRH, MDZ, LZ; Resources: XFL, GL, GQZ, HMZ; Data curation: XRH, ZXI; Writing—original draft: XRH, DZL; Writing—review and editing: DZL, CDB; Supervision: GL, GQZ, HMZ; Project administration: DZL, GQZ and HMZ.



## Conflict of interest

All authors declare that there is no conflict of interest.

## Supplementary Material

Supplementary material can be found at <https://academic.oup.com/cz>.

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