

Lateralized eye use towards video stimuli in bearded dragons (*Pogona vitticeps*)

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Abstract

Lateralized eye use is thought to increase brain efficiency, as the two hemispheres process different information perceived by the eyes. It has been observed in a wide variety of vertebrate species and, in general, information about conspecifics appear to elicit a left eye preference whilst information about prey elicits the opposite. In reptiles, this phenomenon has only been investigated using live conspecifics in agonistic contexts, and so it is not clear whether it can be found when using video stimuli. Here, bearded dragons (*Pogona vitticeps*) were presented with videos of female conspecifics and prey that either moved or were stationary, along with a control video of an empty background. Females exhibited a left eye bias towards conspecifics but males did not, however, both sexes looked at conspecifics significantly longer than prey. Further, animals used their left eye significantly longer when viewing moving stimuli of both categories. These results suggest that, in lizards, lateralized eye use when viewing conspecifics may be controlled by sex, and strongly influenced by stimulus movement. This study therefore provides important insights into the role of lateralized processing in lizard perception, and sets the scene for future work investigating the role of sex on perception of conspecifics and the role of motion in lateralized eye use.

Keywords

Lateralized eye use, perception, bearded dragon, video stimuli

Introduction

Lateralized eye use has been observed in a wide variety of vertebrate species, including mammals (Braccini, Lambeth, Schapiro, & Fitch, 2012; Guo, Meints, Hall, Hall, & Mills, 2009; Racca, Guo, Meints, & Mills, 2012; Smith, Proops, Grounds, Wathan, & McComb, 2016; Versace, Morgante, Pulina, & Vallortigara, 2007), birds (Martinho, Burns, Von Bayern, & Kacelnik, 2014; McKenzie, Andrew, & Jones, 1998; Rogers, 2012; Ventolini et al., 2005; Zucca & Sovrano, 2008), reptiles (Bonati & Csermely, 2011; Hews & Worthington, 2001; Robins, Chen, Beazley, & Dunlop, 2005), amphibians (Vallortigara, Rogers, Bisazza, Lippolis, & Robins, 1998), and fish (Bisazza, De Santi, & Vallortigara, 1999; Bisazza, Facchin, Pignatti, & Vallortigara, 1998; Karenina, Giljov, & Malashichev, 2013). In vertebrates, the right brain hemisphere (which processes information obtained by the left eye) is thought to control emotions and spatial perception, while the left hemisphere (right eye) is responsible for attention, perceptual processing and the control of motor responses (Rogers, Vallortigara, & Andrew, 2013; Vallortigara, Chiandetti, & Sovrano, 2011). Therefore, it has been suggested that lateralized eye use increases brain efficiency, because visual information coming from each eye is processed by different brain regions (Ghirlanda & Vallortigara, 2004; Vallortigara & Rogers, 2005).

Various reptile species are known to show considerable lateralization of their behavior (Rogers et al., 2013; Vallortigara & Rogers, 2005), with information about predators and conspecifics being more easily obtained by the left eye (Bonati, Csermely, López, & Martín, 2010; Hews, Castellano, & Hara, 2004; Hews & Worthington, 2001), and information about prey being more easily obtained by the right eye (Bonati & Csermely, 2011; Bonati, Csermely, & Romani, 2008; Bonati, Csermely, & Sovrano, 2013; Robins et al., 2005). These studies exclusively used live stimuli, with restrained male lizards being used to stage conspecific encounters (Hews et al., 2004; Hews & Worthington, 2001), and live mealworms (*Tenebrio molitor* larvae) used as prey (Bonati & Csermely, 2011; Bonati et al., 2008; Robins et al., 2005).

Previous research investigating conspecific displays and species recognition (Clark, Macedonia, & Rosenthal, 1997; Macedonia & Stamps, 1994; Ord & Evans, 2002; Ord, Peters, Evans, & Taylor, 2002; Van Dyk & Evans, 2007; Yang, Phelps, Crews, & Wilczynski, 2001) has successfully used video stimuli in studies with lizards, focusing on videos of male conspecifics displaying an agonistic visual signal (head bobbing), although one study on social learning in bearded dragons has also shown that these animals are able to imitate female conspecifics seen in videos (Kis, Huber, & Wilkinson, 2015). Therefore, we know that lizards respond to videos of conspecifics, but it is unclear what aspects of the stimulus they are responding to and which information they use from these videos. To test this, we looked at lateralized eye use in bearded dragons (*Pogona vitticeps*) watching and interpreting video stimuli showing conspecifics and prey, that were either moving or stationary.

Bearded dragons originate from central Australia, where they are commonly found in arid areas such as savannas and desert habitats. Their territories overlap and males show strong aggressive behavior towards unfamiliar conspecifics, which often escalates into fights, during which animals can sustain substantial injuries (Rowland, 2009). Therefore, being able to quickly and reliably perceive and respond to conspecifics is beneficial, and eye lateralization has been shown to improve this ability in other lizard species (Bonati et al., 2010; Hews et al., 2004; Hews & Worthington, 2001). Further, bearded dragons eat a wide variety of plant food and are excellent hunters of small animals such as insects, which often move quickly (Oonincx, van Leeuwen, Hendriks, & van der Poel, 2015). Lateralization in eye use has been shown to improve hunting in other lizard species, which predate on similar types of prey (Bonati & Csermely, 2011; Bonati et al., 2008; Robins et al., 2005). Therefore our experiment was designed to investigate (a) whether the response elicited by a female conspecific would be similar to that towards males, as seen in previous research (Hews et al., 2004; Hews & Worthington, 2001), and (b) what level of information is required to elicit any eye preferences. We predicted a right eye preference towards prey if videos are perceived the same way as live stimuli; a left eye preference when observing female conspecifics, if there is no difference in response towards

males and females; and no eye preferences for female conspecifics if the response towards males is caused by the potential for agonistic interaction with them.

Methods

Ten adult (3 males and 7 females, all > one year of age) and nine sub-adults (4 males and 5 females, ca. eight months of age) bearded dragons were used in this experiment. All animals were habituated to being handled by humans on a daily basis. They were housed in groups of 2 to 3 animals per vivarium, males were not kept with other males to avoid aggression. The room temperature was kept at 28°C with additional heat lamps being provided in each vivarium. All vivaria contained UV bulbs. All animals received water ad libitum, vegetables and fruit once per day and live food (crickets and locusts) 3 times per week.

The experiment took place in a rectangular arena (120cm x 40cm) that was separated into two equal compartments by an opaque screen (each compartment measured 60cm x 40cm; Figure 1). At testing, the animals were placed into one compartment, whilst the other compartment held a computer monitor which was used to present the stimuli. The screen separating the two compartments contained a horizontal rectangular hole (3cm x 5cm) through which the animals could see the computer monitor. This peephole constrained the bearded dragons in such a way that made it difficult for the animals to use both eyes simultaneously, making it more likely that they would view the stimuli with only the left or the right eye. It also allowed accurate coding of which eye they were using.

All animals were habituated to the experimental arena before starting the experiment. They were considered habituated when they readily explored and ate live food inside the arena. Each animal was given one trial per day. Each trial consisted of the presentation of one video. The videos were presented using Microsoft PowerPoint. A black screen was displayed while the bearded dragon was

placed in the arena. Animals were placed in the arena facing backwards, away from the peephole. As soon as they turned around and reached the starting position (indicated by markers on the floor of the arena) the video was started manually by the experimenter. Each trial was terminated after the video ended or if the animal failed to reach the starting position within three minutes. Trials in which the animals failed to reach the starting position or in which the animals observed the stimulus for less than three second were discarded and repeated the following day until all animals finished all trials.

Each stimulus was a 15 second video belonging to one of five conditions: stationary prey (either one cricket or one locust, sitting still), moving prey (either a cricket or a locust, running or jumping), stationary conspecific (a female lizard, sitting still), moving conspecific (a female lizard, walking), and an empty background that was used as the control. Each animal was shown three different videos for each condition, and received a total of 15 trials. Four different videos were created per condition to avoid showing animals videos of themselves or highly familiar individuals. Therefore, the video stimuli were allocated to the individuals in a pseudo-random fashion. The order in which the stimuli were presented was also pseudo-randomized, so that no stimuli of the same condition were presented on consecutive days. The order in which the animals were tested was randomized.

The bearded dragons' behavior was recorded using two cameras (Figure 1). A small camera that was installed in front of the monitor recorded the peephole and allowed us to determine precisely which eye they were using, and an overhead webcam was used to record their position, behaviors and head movements.

Data analysis

All recordings were analyzed using Solomon Coder (© András Péter; version beta 15.11.19) to the nearest second. Observed behaviors included the time spent looking with the left eye, the time spent

looking with the right eye, and the total amount of time animals spent looking with either (or both) eyes. Coding was blind to the testing condition. Ten percent of videos were coded for eye use (left, right or both eyes) by a second observer and inter-observer reliability was highly significant (Spearman's correlation: $r_s = 0.93$, $p < 0.001$).

The relative use of the left eye over the right eye was compared between trials using a generalized linear mixed model (using the `glmer` function in the `lme4` package for R version 3.3.1; Bates, Mächler, Bolker, & Walker, 2015), with the time spent using the left eye given the time using the right eye as the binomial response variable, experimental condition (moving or stationary), stimulus species (conspecific or prey) and sex (and all three-and two-way interactions between them) as fixed factors, and individual identity as a random effect to control for the repeated use of subjects between trials. We also included an observation-level random effect term to control for overdispersion (Harrison, 2015). Significance was assessed by comparing the full model to null models lacking the fixed effect of interest using likelihood ratio tests (Crawley, 2011). We also tested whether the proportion of eye use during each condition differed from chance (i.e., a proportion of 0.5) using one-sample t-tests.

Total time spent looking at videos was compared between trials using a linear mixed-effects model (using the `lme` function in the `nlme` package), with log-transformed looking time as the response variable, fixed factors of experimental condition, stimulus species and sex (and their interaction), and individual identity as a random effect. Significance was assessed using F-tests. Comparisons with the empty background control were made using mixed models, as described above, but with only a subset of the relevant data.

We used the marginal coefficient of variation (R^2) as a measure of effect size, calculated using the `r.squaredGLMM` function in the `MuMIn` package (Bartoń, 2016; Nakagawa & Schielzeth, 2013).

Results

Animals looked at the videos on each trial, and spent an average of 11.21 (\pm 0.27) seconds per trial observing the videos. This made up 74.8% of the entire presentation time. The lizards did not frequently switch between eyes and only did so an average of 1.8 ± 0.1 times per trial.

There was no significant three-way interaction for lateralized eye use between sex, condition (moving or stationary) and stimulus species (conspecific or prey), $\chi^2(1) < 0.01$, $p > 0.999$. There were, however, significant two-way interactions between sex and stimulus species, $\chi^2(1) = 11.19$, $p < 0.001$, $R^2 = 0.16$, sex and condition, $\chi^2(1) = 10.96$, $p < 0.001$, $R^2 = 0.17$, and condition and stimulus species, $\chi^2(1) = 11.21$, $p < 0.001$, $R^2 = 0.17$. These interactions are detailed below.

Females used their left eye significantly longer than males when viewing conspecifics, $\chi^2(1) = 24.69$, $p < 0.001$, $R^2 = 0.17$, although there was no significant difference between the sexes when viewing prey, $\chi^2(1) = 0.58$, $p = 0.447$. Females also showed a significantly higher proportion of left eye use when viewing conspecifics than prey, $\chi^2(1) = 30.54$, $p < 0.001$, $R^2 = 0.14$, although there was no significant difference for males, $\chi^2(1) = 0.02$, $p = 0.892$. (Figure 2a).

Females used their left eye significantly longer when looking at moving than stationary stimuli, $\chi^2(1) = 26.66$, $p < 0.001$, $R^2 < 0.01$, but there was no difference for males, $\chi^2(1) = 1.49$, $p = 0.223$. There was also no difference in relative eye use between females and males for stationary, $\chi^2(1) = 2.18$, $p = 0.14$, or moving stimuli, $\chi^2(1) = 0.19$, $p = 0.66$. (Figure 2b).

Animals of both sexes used their left eye significantly more when viewing moving conspecific stimuli than stationary conspecific stimuli, $\chi^2(1) = 12.72$, $p < 0.001$, $R^2 = 0.16$, and moving prey stimuli compared to stationary prey, $\chi^2(1) = 19.31$, $p < 0.001$, $R^2 = 0.18$. There was no significant difference

between stimulus species when they were both moving, $\chi^2(1) = 0.02$, $p = 0.878$, or both stationary, $\chi^2(1) = 2.44$, $p = 0.119$ (Figure 2c).

For the total amount of time the animals spent looking at the stimuli **with the left eye, right eye or both eyes**, there was no significant three- or two-way interactions between sex, condition and stimulus species (all $p > 0.13$). However, animals looked significantly longer at conspecific stimuli compared to prey stimuli, $F_{1,169} = 7.63$, $p = 0.006$, $R^2 = 0.04$ (Figure 3), although there was no difference in looking time between males and females (mean \pm SE, males: 12.0 ± 0.4 s; females, 10.8 ± 0.4 s), $F_{1,17} = 2.66$, $p = 0.121$, or between moving and stationary stimuli (moving: 11.6 ± 0.4 s; stationary, 11.1 ± 0.4 s), $F_{1,169} = 0.29$, $p = 0.589$. When compared to the empty background, animals looked longer at conspecifics (background, 10.7 ± 0.6 s), $F_{1,124} = 4.54$, $p = 0.035$, $R^2 = 0.03$, but not prey, $F_{1,125} = 0.03$, $p = 0.859$ (Figure 3).

Discussion

In contrast to previous research, which focused on the perception of male lizards in videos mostly by other males (Clark et al., 1997; Macedonia & Stamps, 1994; Ord & Evans, 2002; Ord et al., 2002; Van Dyk & Evans, 2007; Yang et al., 2001), this study looked at the perception of females. While it is unclear whether this species can tell the sex of conspecifics from videos, we found that even without strong visual signals typically exhibited by males, such as head bob displays, bearded dragons respond to videos of conspecifics, ruling out the possibility of them recognizing conspecifics only by this characteristic movement. Our results therefore add to the growing evidence that lizards do perceive conspecifics shown in videos as conspecifics.

We found differences between male and female lizards, with females showing a stronger left eye preference for conspecific stimuli than males, a left eye preference for moving stimuli compared to

stationary ones and a left eye preference towards conspecific stimuli compared to prey. Furthermore, there was a general increase in left eye use for moving stimuli irrelevant of whether the stimuli were conspecifics or prey. There was also no difference between males and females in how much attention (measured by time spent looking) they paid to the stimuli, with all animals paying more attention to conspecifics than to prey.

There was a clear difference in how male and female lizards responded to the conspecific stimuli; females showed a significant left eye preference when observing conspecifics whilst males did not. Previous studies investigating lateralized behavior towards conspecifics have presented male stimuli (Hews et al., 2004; Hews & Worthington, 2001) and reveal a left eye preference towards conspecifics. In this experiment, we presented female stimuli to observers of both sexes but only saw a left eye preference in the female observers. This suggests that underlying eye preference, and resultant processing, in lizards may be more complex than previously thought and different contexts may differentially elicit left eye preference in the two sexes.

The role that the behavioral ecology of the species being tested plays on responses remains unclear. However, it offers some potential for interpretation. There is evidence that the left eye/right hemisphere is responsible for the recognition of familiar conspecifics in domestic chicks. Female chicks show preferences for familiar conspecifics, while males often prefer strangers (Vallortigara & Andrew, 1991, 1994). Bearded dragons are territorial, and unfamiliar conspecifics often display aggression towards each other. Unfamiliar conspecifics might pose a greater threat to females than to males, as females are generally smaller and therefore more vulnerable to attacks. Therefore, use of the left eye over the right eye may enhance females' ability to distinguish familiar from unfamiliar conspecifics. For future studies, it would therefore be interesting to compare lateralized eye use towards familiar and unfamiliar conspecifics, and test their ability to distinguish familiar and unfamiliar conspecifics with either eye. It is also possible that the findings may be the result of same-sex

competition, however, more work is required before this can be ascertained. It is clear, however, that the difference was not controlled by attention, as we found no difference in the amount of time that males and females looked at the conspecific videos. Further, lizards looked at the videos depicting conspecifics longer than those depicting prey, suggesting that they were processing information from these stimuli.

While we expected a left eye preference for videos of conspecifics (Hews et al., 2004; Hews & Worthington, 2001), it was surprising to find preferential left eye use for videos of moving prey. Most research shows right eye preferences for prey stimuli (Bonati & Csermely, 2011; Robins et al., 2005; Vallortigara et al., 1998). However, the difference in eye use between stationary and moving stimuli suggests that this finding is likely to be an effect of movement. Prey movement has been shown to directly influence predatory behavior in lizards (Hoese, Peters, & Evans, 2008). Though bearded dragons do eat stationary plant food, they respond very strongly to prey movement. It is therefore possible that these stimuli might have been perceived and processed differently when moving. Previous studies which investigate lateralized eye use in lizards towards prey used meal worms as stimuli (Bonati & Csermely, 2011; Bonati et al., 2008; Robins et al., 2005). Mealworms move in a very different way to crickets and locusts and thus the impact of motion may not have previously been observed. Further work on prey perception should investigate the role of prey type and motion on stimulus perception.

In summary, this study provides important insights into the role of lateralized processing in lizard perception and sets the scene for future work investigating the role of sex on perception of conspecifics and the role of motion in lateralized eye use.

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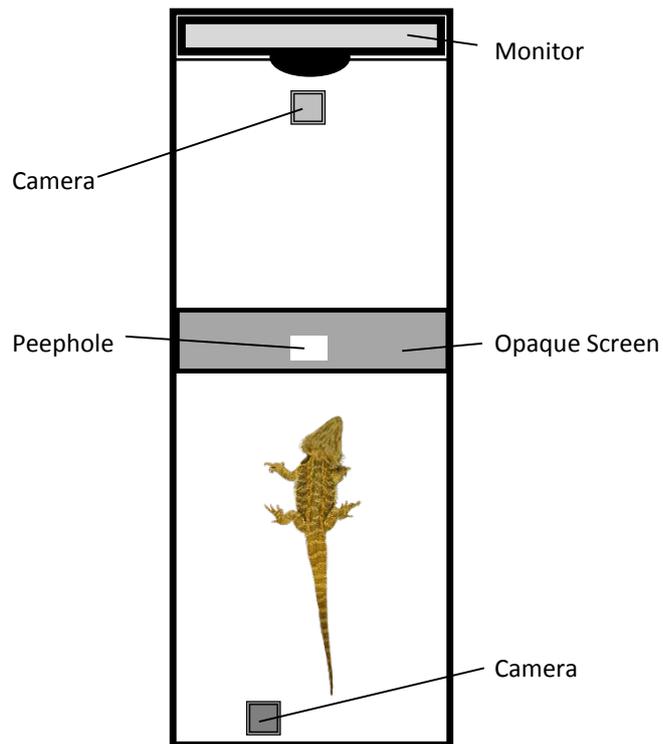


Fig.1.: Experimental setup, consisting of a rectangular arena, a computer monitor and an opaque screen with a peephole.

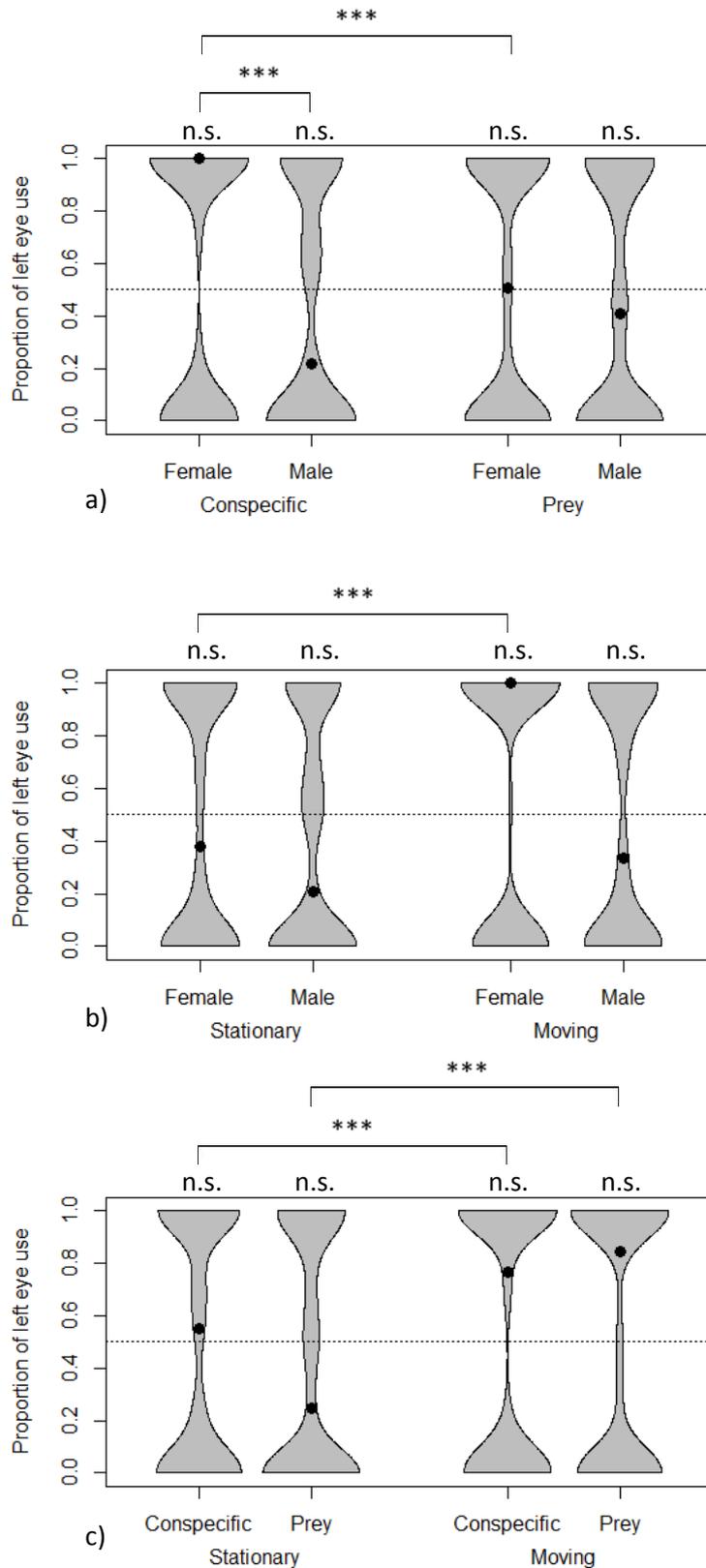


Fig.2: Proportion of left eye use for different stimuli. Beanplots (Kampstra, 2008) showing the proportion of left eye use as a function of (a) stimulus species (conspecific or prey) and sex, (b) condition (moving or stationary) and sex, and (c) condition and stimulus species. Shaded areas show the estimated density of the underlying distributions, black dots indicate medians, and the horizontal

dashed line indicates chance levels of eye use. Asterisks above the boxes indicate differences from chance; lines above bars indicate significant pairwise differences: *** $p < 0.001$; n.s. non-significant.

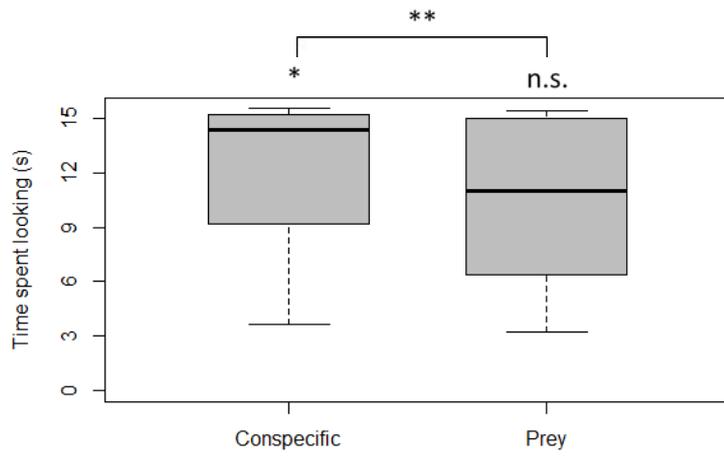


Fig. 3: Amount of time spent looking at conspecific and prey stimuli. Asterisks above the boxes indicate differences from the empty background (control) trials; line above bars indicates significant differences between stimulus species: * $p < 0.05$; ** $p < 0.01$; n.s. non-significant.