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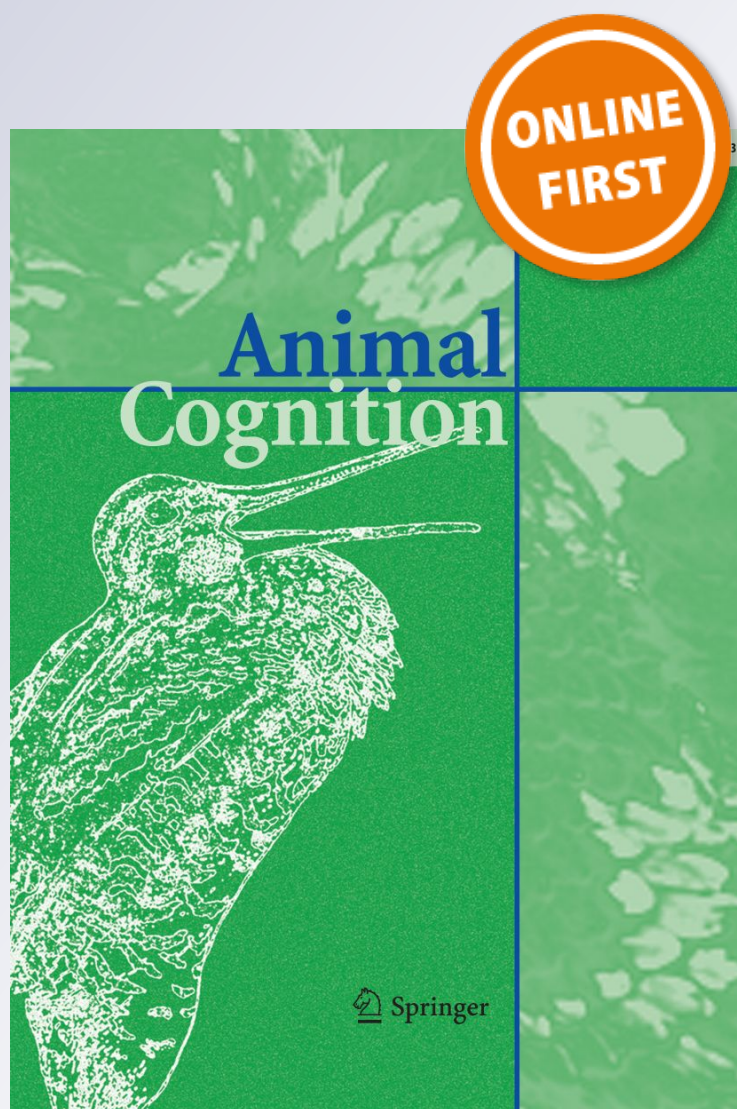
**Andrey Giljov, Yegor Malashichev & Karina Karenina**

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# What do wild saiga antelopes tell us about the relative roles of the two brain hemispheres in social interactions?

Andrey Giljov<sup>1</sup> · Yegor Malashichev<sup>1,2</sup> · Karina Karenina<sup>1</sup> Received: 5 November 2018 / Revised: 31 March 2019 / Accepted: 3 April 2019  
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## Abstract

Two brain hemispheres are unequally involved in the processing of social stimuli, as demonstrated in a wide range of vertebrates. A considerable number of studies have shown the right hemisphere advantage for social processing. At the same time, an approach–withdrawal hypothesis, mainly based on experimental evidence, proposes the involvement of both brain hemispheres according to approach and withdrawal motivation. The present study aimed to test the relative roles of the two hemispheres in social responses displayed in a natural context. Visual biases, implicating hemispheric lateralization, were estimated in the social interactions of saiga antelope in the wild. In individually identified males, the left/right visual field use during approach and withdrawal responses was recorded based on the lateral head/body position, relative to the conspecific. Lateralized approach responses were investigated in three types of interactions, with left visual field bias found for chasing a rival, no bias—for attacking a rival, and right visual field bias—for pursuing a female. In two types of withdrawal responses, left visual field bias was found for retreating after fighting, while no bias was evident in fight rejecting. These findings demonstrate that neither the right hemisphere advantage nor the approach–withdrawal distinction can fully explain the patterns of lateralization observed in social behaviour. It is clear that both brain hemispheres play significant roles in social responses, while their relative contribution is likely determined by a complex set of motivational and emotional factors rather than a simple dichotomous distinction such as, for example, approach versus withdrawal motivation.

**Keywords** Laterality · Hemispheric specialization · Brain asymmetry · Eye preference · Ungulate · Contest behaviour

## Introduction

Lateralized social processing has been found across a wide variety of animal species. Asymmetric involvement of the left and right brain hemisphere is evident in numerous aspects of social cognition such as, for example, recognition of conspecifics, spatial coordination with them during synergistic activities, decoding of social signals, and

learning social hierarchies (for reviews, see, e.g., Brancucci et al. 2009; Rosa Salva et al. 2012; Lindell 2013). This is not surprising since social coordination is assumed to serve as a driving force for the evolutionary emergence of one-sided population-level biases in lateralized behaviour (Ghirlanda and Vallortigara 2004; Vallortigara and Rogers 2005; Ghirlanda et al. 2009). In animal behaviour, lateralized implementation of socially relevant functions can be manifested as the left or right visual field advantage for the processing of social information. First revealed using an experimental approach (Howard et al. 1980; Bullock and Rogers 1992), the lateralized social processing is now known to determine the spatial positioning of the individual in the social environment in natural settings (e.g., Baraud et al. 2009; Quresmini et al. 2014; Ventolini et al. 2005). As proven by a wide range of studies (for reviews, see Rogers et al. 2013; Vallortigara and Versace 2017), one-sided preferences in spatial positioning relative to a stimulus are underpinned by processing visual information predominately through the left or right visual field and right or left hemisphere, respectively. Within

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✉ Karina Karenina  
angil\_1305@mail.ru; k.karenina@spbu.ru

<sup>1</sup> Department of Vertebrate Zoology, Faculty of Biology, Saint Petersburg State University, Universitetskaya Nab., 7-9, Saint Petersburg 199034, Russia

<sup>2</sup> Laboratory of Molecular Neurobiology, Department of Ecological Physiology, Institute of Experimental Medicine, Saint Petersburg, Russia

this context, preferences for a particular lateral position in social interactions reflect brain lateralization for encoding of social information in the appearance and behaviour of conspecifics (e.g., Baraud et al. 2009; Rosa Salva et al. 2012; Versace et al. 2007). Such positional preferences exist, for example, in great apes. The investigation of spontaneous interactions within the social groups of captive gorillas and chimpanzees revealed a significant group-level preference for focal individuals to keep conspecifics positioned on their left side compared with their right side (Quaresmini et al. 2014). The interpretation of the asymmetrical positioning of the individual relative to a conspecific from the point of view of sensory lateralization is supported by the studies showing that the positional preferences displayed in a social context are absent in non-social contexts (Karenina et al. 2017; Forrester et al. 2014).

One-sided behavioural biases associated with visual lateralization are especially pronounced and easily revealed using observational methods in the social behaviour of species with laterally placed eyes and a small binocular overlap (Rogers 2017). Indeed, robust preferences for keeping the mother on the left side (primarily in the left visual field) have been found in infants of diverse mammal species with laterally placed eyes, such as, for example, muskox, orca, walrus, and red kangaroo (Karenina and Giljov 2018; see Kaplan 2017 for a similar preference in juvenile birds). In adult mammals with laterally positioned eyes, preference to keep group mates on the left side in a variety of circumstances has been shown in horses (Austin and Rogers 2014; Farmer et al. 2018) and common elands (Bordes et al. 2018).

A plethora of empirical evidence from humans and other species indicates right hemispheric dominance for a great variety of social cognition tasks (e.g., Brancucci et al. 2009; Forrester and Todd 2018). For example, discrimination of emotional scenes in humans is more accurate and faster when the emotional scene appears in the left visual field (right hemisphere) as compared with the right visual field (left hemisphere) (Calvo et al. 2015). The model positing the right hemisphere advantage for social (emotional) processing is opposed by the hypothesis proposing the involvement of both brain hemispheres according to approach and withdrawal motivation (reviewed in Najt et al. 2013). Evidence for an approach–withdrawal distinction in cerebral lateralization suggests that the right hemisphere activity is associated with avoidance motivation and the left hemisphere activity is associated with approach motivation (Harmon-Jones 2004; Kelley et al. 2017). In line with this model, Australian magpies use the right eye when approaching a predator, but shift to the left eye use prior to moving away for escaping from it (Koboroff et al. 2008). In a social context, the similar tendency has been revealed in experiments on domestic dogs, with a left gaze bias (right hemisphere dominance)

found in looking at threatening (aggressive) facial expressions of conspecifics and a right gaze bias (left hemisphere dominance)—towards friendly ones (Racca et al. 2012). In addition to the right hemispheric and approach–withdrawal hypotheses, other factors such as, for example, emotional valence (reviewed in Najt et al. 2013) and familiarity (Peirce et al. 2000) of the social stimulus have been suggested to impact on the manifestation of lateralization in social behaviour.

Conflicting evidence makes the relative involvement of the left and the right hemisphere in social processing far from clear (Najt et al. 2013). Social animals are constantly faced with approach/withdrawal choices when interacting with conspecifics that offer an opportunity to test the existing hypotheses about the roles of two hemispheres in social behaviour in naturalistic settings. While extensive experimental research has been conducted to date (reviewed in Rosa Salva et al. 2012), there is a paucity of naturalistic investigations in this area. In the present study, we aimed to test in a natural context whether the right hemisphere is dominant in social processing regardless of motivation or, alternatively, two hemispheres are differentially involved according to approach/withdrawal motivation. With this aim, spontaneous social behaviours were investigated in critically endangered saiga antelope (*Saiga tatarica tatarica*),

*Saiga tatarica tatarica* is a nomadic bovid inhabiting the semi-arid rangelands of central Asia and the pre-Caspian (Bekenov et al. 1998). A drastic decline of the global population has led to a Critically Endangered listing on the 2002 IUCN Red List (Milner-Gulland et al. 2003). The most recent sudden decline of saiga population in the pre-Caspian has been argued to be caused by a catastrophic drop in the number of adult males owing to selective poaching for the horns (Milner-Gulland et al. 2003; Neronov et al. 2013). In this harem-breeding ungulate, an adult male typically defends a harem of 12–30 females during the rut which takes place in December (Bekenov et al. 1998; Sokolov and Zhirnov 1998). Nowadays, the sex ratio is heavily biased towards females by selective poaching that likely results in a significant number of non-reproducing females (Milner-Gulland et al. 2003). Once the rut is over, the harems may join together to form large groups. Group size and composition vary significantly depending on the climate, food and other factors (Bekenov et al. 1998; Gilev and Karenina 2015; Karimova and Lushchekina 2018). According to the most recent study, small (21–200 individuals) and very small (1–20 individuals) saiga groups constitute 80–90% of the population in the northwestern pre-Caspian region of Russia throughout the year (Karimova and Lushchekina 2018). While fights between males and male–female chasing are most pronounced during the rut, these types of interactions are often observed at other times of the year (Gilev and Karenina 2015).



Saiga antelope has been proven to be a good model species for investigation of lateralized social interactions. A previous research showed visual lateralization in saiga calves interacting with their mothers (Karenina et al. 2017). A variety of social contacts which include approach and withdrawal responses make a highly social saiga antelope particularly suitable for the specific aims of the present study. Laterally placed eyes and protruding orbits provide saiga antelopes with a wide field of vision (Kiley-Worthington and de la Plain 1983; Teer et al. 1996). In bovids, visual information coming from the left visual field is primarily transferred to the animals' contralateral brain hemisphere and vice versa, because of the high degree of decussation of the optic nerves in the optic chiasm (Herron et al. 1978; Phillips et al. 2015). Thus, the characteristics of Saiga's visual system suggest that one-sided biases in the use of their lateral visual fields can be interpreted as manifestations of hemispheric lateralization.

In this study, we assessed saiga males' preferences for left/right visual field use during approach and withdrawal responses performed in different social contexts. The right hemisphere hypothesis predicts preferential use of the left visual field in all types of social responses, whereas the approach-withdrawal hypothesis predicts the right visual field bias for approaches and left visual field bias for withdrawal responses. The observed visual lateralization of saiga males did not unequivocally support any of the hypotheses, with only some of the lateral preferences distributed in line with the predictions.

## Methods

### Study site and subjects

The data on wild saiga antelopes were collected at Stepnoi State Nature Sanctuary, Astrakhan oblast (45°58'N, 46°33'E) in the steppes of the northwestern pre-Caspian region of Russia. Observations were made from a small (approximately 2.4 × 1.5 m) stationary wooden hide covered with camouflage net to minimize visual contrast with the surrounding environment. The hide was only 50 cm higher than the ground level because the main part of it was underground. The hide was situated near an artesian well extensively used by the local saiga antelope population as a source of drinking water, mineral lick, resting place, and social arena (Gilev and Karenina 2015). On average, five hundred saigas, including single individuals, same- and mixed-sex groups visited the well daily during the period of data collection. In hot weather, more than 1500 individuals per day have been recorded. Saiga antelopes (estimated population size—5000 individuals) travel across the territory of the sanctuary throughout the year (Karimova and Lushchekina

2018) that resulted in many different individuals visiting the site during the period of data collection. Flat banks of the waterhole with lack of vegetation provide an open area for a variety of within- and between-group social interactions and enable continuous observations of focal individuals (Gilev and Karenina 2015). The hide was set up 2 years before the beginning of the study, and saigas were well habituated to the hide approaching it at a distance of 5–10 m without any signs of disturbance. Observers entered the hide in low light in the early morning to minimize disturbance. The set of natural markings such as scars and individual features in colouration and shape of the horns was used for photo-identification of individual males. The age class of males was recognized based on the length of their horns. Two clearly distinguishable age classes (1-year-old males and males, two and more years old) were present owing to highly synchronous calving in this species (Milner-Gulland 2001). One-year-old males were clearly distinguished from the older males by the size and shape of the horns (Sokolov and Zhirnov 1998).

### Data collection

The data collection was carried out for 35 days in May 2015, 20 days in May 2016, and 15 days in May 2018. Dyadic interactions of saiga males with male and female conspecifics were recorded based on scan sampling method (Altman 1974) for approximately 10 h per day during periods of high animals' activity in the morning (between 3:30 a.m. and 11:00 p.m.) and in the afternoon (between 17:00 a.m. and 19:30 p.m.). No data were recorded in poor visibility conditions. Scores were recorded using pen and paper by two observers continuously monitoring the behaviour of male saigas in the study area (usually no more than five at the same time). Binoculars (12× magnification) were used if needed and social interactions were video recorded whenever possible. The video recording of all interactions was not conducted, since the use of the camera was restrained by the construction of the hide. It was not possible to record data blind because the study involved focal animals in the wild.

Over 710 h of observation were conducted, with 245 events of left/right visual field use recorded. Inter-rater reliability was assessed for the first 50 events observed. The categorical coding of visual field use (left/right/non-lateral) performed independently by two raters was compared using kappa statistics, resulting in 92% reliability ( $\kappa=0.86$ , SE of  $\kappa=0.065$ ; 95% CI 0.74 to 0.99).

The methods used in the present study are generally similar to those used previously in the study of lateralized positioning of saiga calves relative to their mothers (Karenina et al. 2017). Lateral head or whole body position, relative to the conspecific, was used to determine the left/right visual field use. High-intensive dyadic

interactions with distinct approach/withdrawal responses in which relative roles of two participants can be clearly recognized by the observer were investigated. The first left/right visual field use in every dyadic interaction was recorded. Much like in the previous studies of ungulate social lateralization (Austin and Rogers 2012, 2014), eye use was recorded when a focal animal kept its opponent's in the left or right visual field immediately before and during social responses. Using photo-identification, repeated observations of the same individuals were excluded to avoid pseudoreplication (only one response per individual male was used in the analysis). In every interaction, the score from only one individual in a dyad was recorded. All the types of the behavioural responses studied implied only one individual in a dyad to actively choose the lateral position relative to a partner. No behaviours in which both individuals simultaneously took a lateral position relative to each other were studied.

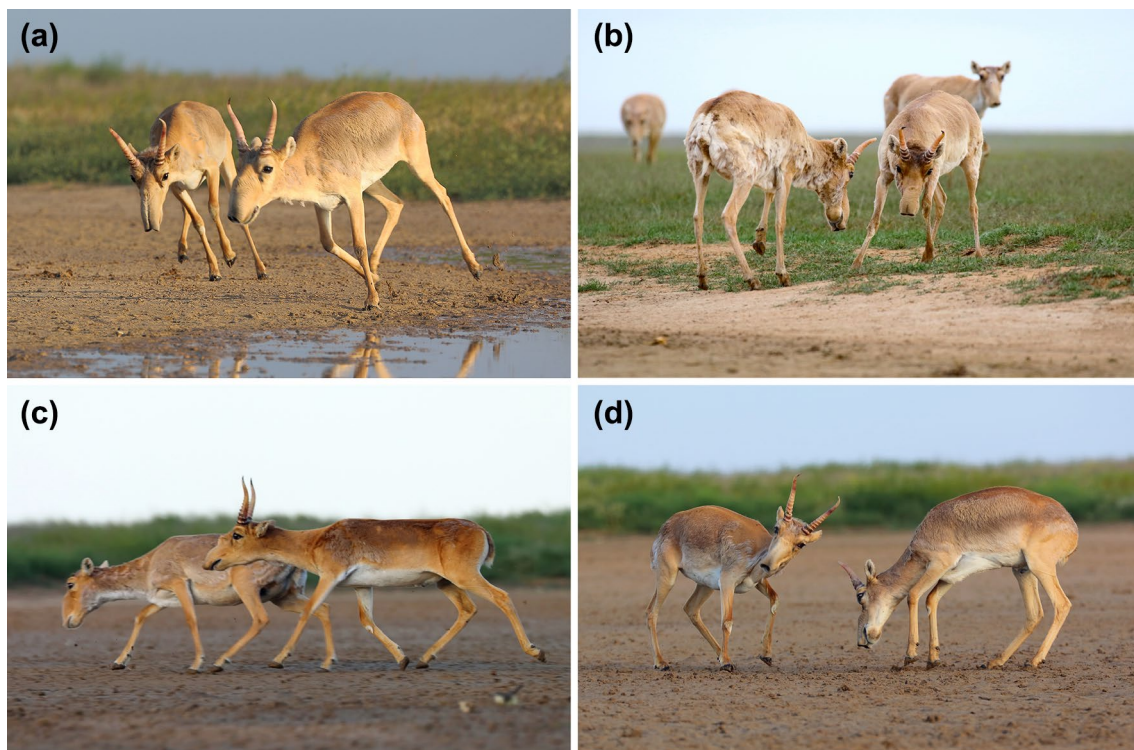
Since natural markings can potentially be unstable over long periods of time, individual photo-identification was applied only for the recognition of males observed during one study period (15–30 consecutive days in each year of study). Only 1-year-old males were observed in 2016 and 2018 to exclude the probability of the repeated sampling of the individuals observed in the previous year of study.

## Types of interactions

### Approach

Lateralized approach responses were investigated in three types of interactions, namely when (1) chasing a rival, (2) attacking a rival, and (3) pursuing a female. The use of the left/right visual field during chasing a rival was recorded when a focal male took a lateral position relative to another male running after him typically to drive him away from females (Fig. 1a).

Attacking a rival was observed during face-to-face fights between two males. In saiga fights, one of the males often put its head laterally to the rival's head, then approach it rapidly and hit it with the horns. As a very common element of saiga fighting behaviour, the lateral head positioning relative to a rival was used as a demonstration of potentially lateralized behaviour. The lateral head positioning in fighting saiga antelopes closely resembles some of the types of the attack previously studied for visual lateralization in domestic and Przewalski's horses (Austin and Rogers 2012, 2014). In contrast to horses, however, the saiga rivals often faced each other frontally for head-butting at the later stages of the attack. In attacking a rival, one visual field use was recorded when a focal male positioned its head laterally relative to the



**Fig. 1** Types of dyadic interactions in which visual lateralization in saiga males was assessed, **a** chasing a rival, **b** attacking a rival, **c** pursuing a female **d** retreating (a male on the left side of the image is starting a movement away from the rival)

head of the rival immediately before the focal male hit the rival with its horns (Fig. 1b).

Pursuing a female was defined as follows: a male running after a female with its head up and proboscis raised. Such chasing, often referred as herding behaviour (Underwood 1982), helps males to keep females together and is observed throughout the year, while the mating itself takes place only during the rut in winter (Bekenov et al. 1998). The use of the left/right visual field in this behaviour was recorded when the male took a lateral position relative to the female during the chase (Fig. 1c).

### Withdrawal

Lateralization of withdrawal responses was assessed in two types of interactions, (1) retreating and (2) fight rejecting. We recorded the lateral position of the withdrawing individual relative to a partner taken from an initially symmetrical face-to-face position of two males. Retreating was defined as male's movement away from the rival which characterized the termination of a face-to-face fight between two males (Fig. 1d). The male was considered retreating only if it then ran away and was chased by the rival. Lateral head position relative to a rival prior to withdrawing from it was used as a behavioural marker of one visual field use by the retreating male.

Fight rejection comprised a male turning away from another male approaching it frontally and inviting it to fight by typical agonistic displays such as head shakes and body-jerking movements (Fig. S1). Left/right visual field use was estimated based on the side of the body the rejecter exposed to the inviter when turning away.

### Ethical statement

The ethical permission for the study was obtained from the St. Petersburg State University ethical committee (permit no. 131-03-4). Work was conducted with the approval of Stepnoi State Nature Sanctuary authorities. The study was purely observational. The observations were conducted from the hide that kept the disturbance of the antelopes to a minimum.

### Data analysis

The possible effects of the type of interaction, males' age class and the year of the study (2015, 2016, 2018) on lateralization were assessed using a binary logistic regression with the visual field use (left, right) as the dependent variable. Post-hoc testing (Tukey's Honest Significant Difference Test) was used to reveal a clearer pattern of factors' effect on laterality. Laterality Index (LI) scores were calculated using the formula  $[LI = (R - L)/(R + L)]$ , with  $R$  and  $L$  corresponding to the frequency counts for right and left visual field use. LI scores ranged from  $-1.0$  to  $+1.0$ , with negative values reflecting the left bias and positive values reflecting the right bias. The significance of biases for males using the left/right visual field in each type of interactions was tested using a binomial  $z$  test. All statistical tests were two-tailed, alpha level ( $\alpha$ ) was set at 0.05, and CI at 95%. The analyses were conducted using the JASP Statistical Analysis (ver. 0.9.0.1; <https://jasp-stats.org/>).

### Data availability

All data generated or analyzed during this study are included in this published article and its Supplementary Information file.

### Results

In total, the observations of 245 individual males (one score per individual) were included in the analysis. The sample sizes varied according to the type of interactions (see Table 1).

The binary logistic regression model was used to examine factors that influenced the odds to use the right visual field during a focal observation. The model included the left/right visual field use as a dependent variable and the following fixed factors: type of interactions, age class, and year of study (see Supplementary Information). The test of the full model was found to be significant ( $\chi^2 = 107.55$ ,  $p < 0.001$ , Nagelkerke  $R^2 = 0.47$ ) and showed a significant difference in lateralization between the studied types of interactions ( $p < 0.05$ ). Other factors examined had no appreciable effect

**Table 1** Raw frequencies, binomial approximations of  $z$  scores and LI scores for each type of interaction

Type of interaction	Chasing a rival	Attacking a rival	Pursuing a female	Retreating	Fight rejecting
Right visual field	10	39	51	4	11
Left visual field	43	41	3	27	16
Laterality index	-0.62	-0.03	0.89	-0.74	-0.19
Binomial $z$ score	-4.40	-0.11	6.40	-3.95	-0.77
$p$ value	<0.001	0.911	<0.001	<0.001	0.442

The number of scores is equal to the sample size (one score per individual)

on laterality ( $p > 0.05$ ). Thereupon we performed a backwards elimination model selection to find the parsimonious model which showed the significant effect of an interaction type on lateralization ( $p < 0.001$ ; see Supplementary Information). The Tukey's post hoc pairwise comparisons revealed significant differences between pursuing a female and all other types of interactions ( $p < 0.001$ ). Significant differences were also found between attacking and chasing a rival, and between attacking and retreating ( $p < 0.001$ ). The rest of the pairwise comparisons were non-significant ( $p > 0.05$ ; see Supplementary Information).

Further analysis showed a significant bias for saiga males using their left visual field when chasing a rival ( $n = 53$ ;  $p < 0.001$ ) and retreating ( $n = 31$ ;  $p < 0.001$ ). In contrast, males used the right visual field significantly more often than the left visual field when pursuing a female ( $n = 54$ ;  $p < 0.001$ ). No significant visual bias was found in attacking a rival ( $n = 80$ ;  $p > 0.05$ ) and fight rejecting ( $n = 27$ ;  $p > 0.05$ ; Fig. 2). Raw frequencies, binomial approximations of  $z$  scores and LI scores for each type of interactions are presented in Table 1.

## Discussion

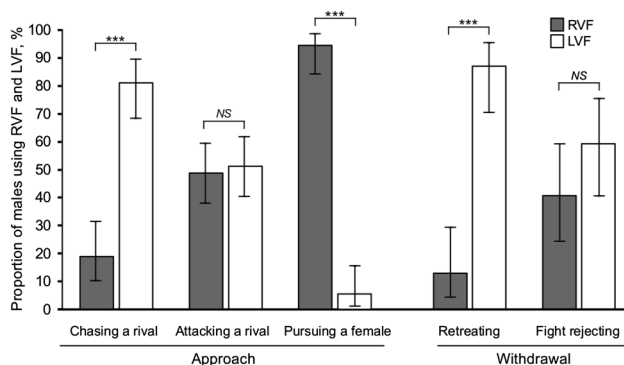
According to the widely accepted concept, one-sided visual bias in monitoring the partner during social responses implies an advantage of the contralateral hemisphere for the control of this type of responses (e.g., Austin and Rogers 2014; Farmer et al. 2018; Rosa Salva et al. 2012; Versace et al. 2007). The results from this study show visual lateralization in male saiga antelopes varying according to the type of the social interaction. According to the right hemisphere hypothesis, a generalized left visual field (right hemisphere) bias is predicted in social responses (e.g., Brancucci et al. 2009; Forrester and Todd 2018). In contrast, the direction of visual preferences in male saigas depended on the context of

the interaction. All three possible patterns of lateralization (left visual field bias, right visual field bias, and no bias) were displayed in different types of social interactions.

These results, along with many previous findings (e.g., Rosa Salva et al. 2012), demonstrate that considering various social responses together is not a useful framework for understanding the lateralization of social processing. As our study confirms, the fact that the particular response is an element of social behaviour do not allow to predict that this response is under the predominant control of the right hemisphere.

According to the second hypothesis considered, the right visual field bias is expected in interactions involving an approach to the conspecific, while the left visual field bias is expected for interactions involving withdrawal from the conspecific (e.g., Harmon-Jones 2004; Kelley et al. 2017). Contrary to the prediction, the visual preferences in male saigas were not distributed according to the approach–withdrawal distinction (see Fig. 2). Lateralization of both approach and withdrawal responses differed between the types of social interactions. Among the interactions belonging to the approach category, a left visual field bias was found for chasing a rival, no bias—for attacking a rival, and a right visual field bias for pursuing a female. The results of the previous study also contradict the approach–withdrawal hypothesis, with the left visual field preference found in saiga antelope calves approaching their mothers (Karenina et al. 2017). In two types of withdrawal responses investigated in the present study, left visual field bias was shown for retreating after fighting, while no bias was evident in fight rejecting. Thus, despite the fact that approach and withdrawal motivations are a fundamental mechanism of individual survival, this motivational distinction did not fully explain the observed pattern of lateral visual biases. Neither of the two widely discussed hypotheses of lateralized socio-emotional processing is unequivocally supported by the complex pattern of lateralized responses in saigas' intraspecific interactions in the wild.

Oppositely directed visual biases in some behaviours of male saigas imply the division of roles between the hemispheres and demonstrate that both hemispheres significantly contribute to the control of social responses. Saiga males demonstrated a significant right visual field bias for pursuing a female during herding (i.e. putting females together, close to each other). The left hemisphere, which primarily processes input from the right visual field, plays a dominant role in the allocation of stimuli into categories and control of established patterns of behaviour (Vauclair et al. 2006; Rogers et al. 2013). The left hemisphere advantage for category-based distinctions, including those performed in a social context (Rosa Salva et al. 2012), may facilitate males' recognition of mature females versus males and immature individuals via the right visual field. Indeed, in many vertebrate



**Fig. 2** Overall proportion of saiga males using the right visual field (RVF) and the left visual field (LVF) by interaction type and approach/withdrawal response. \*\*\* $p < 0.001$ , NS non-significant



species, the left hemisphere controls the responses based on the innate or experience-dependent recognition of particular characteristics of a social stimulus used to assign it to a category, such as releaser cues (Rosa Salva et al. 2012, but see Karenina et al. 2013 for an exception in fish). Furthermore, in saiga males, the greater left hemispheric involvement may favour the fulfilling of a female pursuit, since sustaining a course of actions and avoidance of distraction is a function of the left side of the brain (Rogers et al. 2013). It is possible that similar cerebral mechanisms underlie the pursuit of females as well as the pursuit of prey, and the latter is a well-known competence of the left hemisphere (Rogers et al. 2013).

A significant bias for males using a left visual field when chasing a rival and retreating after a fight corresponds with the general vertebrate model which attributes the processing of fear- and aggression-inducing stimuli to the right hemisphere functions (Rogers 2002). The monitoring of the opponent via the left visual field can confer benefits to saiga males because of the right hemisphere advantage for the perception of the threat level of conspecific behaviour (Bordes et al. 2018; Forrester and Todd 2018). It is unclear, however, why the significant visual bias is lacking in other types of male–male interactions such as attacking a rival and fight rejecting. A turning away from another male during the fight rejecting is a less vigorous and likely less emotional response than the other responses studied. Consequently, motivation and arousal during the fight rejecting may not be strong enough to evoke a lateralized response. In contrast, attacking a rival during a face-to-face fighting is associated with relatively high levels of arousal, and the absence of lateralization here could be explained by the factors not analyzed in this study. The visual field used by the focal male was recorded prior to hitting the rival. Potentially, the lateral head position was determined to a greater extent by the individual's preferred/stronger side to initiate a hit (or any other motor bias) than the visual preference per se. Notably, domestic pigs also show no lateral preference for body orientation towards the opponent during contest behaviour (Camerlink et al. 2018).

Besides the approach–withdrawal distinction discussed earlier, social motivations can be categorized according to its valence. The valence-specific hypothesis proposes that the left hemisphere is dominant for processing positive emotions and the right hemisphere is dominant for negative emotions (reviewed in Najt et al. 2013). A distinction of emotional valence can be apparent in experimental studies such as those investigating processing of emotional scenes (Calvo et al. 2015) or facial expressions (Wedding and Stalans 1985; Racca et al. 2012; Siniscalchi et al. 2018). However, positive versus negative categorization seems to be less applicable to the interpretation of animal behaviour in a natural context. The emotional valences of

the behavioural responses studied in the present study are not explicit. Potentially, all male–male interactions can be considered as negative since they are associated with competitive agonistic behaviour, while pursuing a female can be perceived as a more positively valenced male behaviour. If this is true, our results are partially consistent with the valence-specific hypothesis, with the right visual field bias found in males' behaviour towards females and left visual bias found in two of four types of interactions with males. On the other hand, males were observed in non-rutting season and, consequently, the level of aggressiveness (and negativity) in behaviours associated with fighting might be relatively low. Moreover, the context of some of the male–male interactions suggests that their emotional valence may be positive rather than negative. This may be the case, for example, for the chasing of a retrieving rival by a winner. A further argument against the valence-specific explanation comes from the previous study of lateralized behaviour of saiga calves. Contrary to the prediction of the valence-specific hypothesis, saiga calves preferred to keep the mother, an apparently positive stimulus, in their left visual field (Karenina et al. 2017). Acknowledging the vague determination of emotional valence of animal behaviours in the wild, we assume that the patterns of visual lateralization in the saiga antelope are unlikely explained by the valence-specific hypothesis.

Finally, our findings in a non-primate mammal in the wild are in line with the experimental results on humans showing that the most widely discussed theories of lateralized social processing cannot fully and clearly explain current empirical evidence (e.g., Thomas et al. 2014; Prete et al. 2015). The manifestation of visual lateralization in saigas varied according to the social context of the interaction, suggesting that both brain hemispheres impact significantly on social processing. The relative contribution of two hemispheres appears to be strongly dependent on specific motivational and emotional characteristics of the social response. The advantage of one or the other hemisphere for the particular social response displayed by an animal in a natural setting is likely determined by a multifaceted mechanism rather than a simple categorical distinction such as approach versus withdrawal motivation or positive versus negative affect.

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## Compliance with ethical standards

**Conflict of interest** The authors declare that they have no conflict of interest.

**Ethical approval** All applicable international, national, and institutional guidelines for the care and use of animals were followed. All procedures performed in the study were in accordance with the ethical standards of the St. Petersburg State University ethical committee (Permit No. 131-03-4).

**Informed consent** Informed consent is not applicable to the study since no human subjects were included in the study.

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