Differential roles of the right and left brain hemispheres in the social interactions of a free-ranging ungulate

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A B S T R A C T

Despite the abundant empirical evidence on lateralized social behaviours, a clear understanding of the relative roles of two brain hemispheres in social processing is still lacking. This study investigated visual lateralization in social interactions of free-ranging European bison (*Bison bonasus*). The bison were more likely to display aggressive responses (such as fight and side hit), when they viewed the conspecific with the right visual field, implicating the left brain hemisphere. In contrast, the responses associated with positive social interactions (female-to-calf bonding, calf-to-female approach, suckling) or aggression inhibition (fight termination) occurred more likely when the left visual field was in use, indicating the right hemisphere advantage. The results do not support either assumptions of right-hemisphere dominance for control of various social functions or hypotheses about simple positive (approach) versus negative (withdrawal) distinction between the hemispheric roles. The discrepancy between the studies suggests that in animals, the relative roles of the hemispheres in social processing may be determined by a fine balance of emotions and motivations associated with the particular social reaction difficult to categorize for a human investigator. Our findings highlight the involvement of both brain hemispheres in the control of social behaviour.

1. Introduction

A wide range of social behaviours and underlying brain functions are lateralized in mammals (Brancucci et al., 2009; Lindell, 2013). These lateralizations can manifest as, for example, preferences to monitor conspecifics with one eye or visual field (Rogers, 2017). In social groups, visual lateralization can induce consistent lateral biases in the spatial positioning of the individuals relative to their group members (Forrester and Todd, 2018). Significant preferences for focal individuals to keep group mates positioned on their left side compared with their right side has been found in a range of mammalian species (Quaresmini et al., 2014; Bordes et al., 2018; Farmer et al., 2018). The same biases have been found in dyadic interactions between adult individuals (e.g., Austin and Rogers, 2014; Boeving et al., 2017) and between parent and offspring (Karenina and Giljov, 2018). Such one-sided positional preferences act as informative behavioural markers of cerebral lateralization, especially in species with laterally placed eyes in which nerve fibres from one visual field project predominantly to the opposite side of the brain (Rogers et al., 2013; Rogers, 2017; Vallortigara and Versace, 2017).

Numerous examples of right hemisphere advantage for social processing are found in human (Brancucci et al., 2009) and non-human studies (Forrester and Todd, 2018). It is widely recognized that the right hemisphere, implicating the left visual field use, is dominant for the encoding of social information in the appearance and behaviour of conspecifics, especially when the assessment of potential threat is crucial (Rogers et al., 2013). Nevertheless, the relative roles of two brain hemispheres in social processing seem to be equivocal. While some empirical evidence suggests the right hemisphere advantage for any social response (e.g., Farmer et al., 2018), other implies that the involvement of the left or right hemisphere depends on the context of social response.

The division of functions between the two hemispheres has been suggested to follow such dichotomous distinctions as approach/withdrawal or positivity/negativity (Najt et al., 2013). Approach and withdrawal reactions, being a fundamental mechanism of individual survival, were proposed to be controlled by different hemispheres such that the left hemisphere is dominant for approach and the right hemisphere is dominant for withdrawal (Kelley et al., 2017). Generally consistent with this is the valence hypothesis which purports that negative emotions are processed and controlled by the right hemisphere and positive emotions by the left hemisphere (Davidson, 1995). For

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example, domestic dogs demonstrate a left gaze bias (right hemisphere dominance) when looking at conspecifics with threatening (aggressive) facial expressions of and a right gaze bias (left hemisphere dominance) when looking at friendly conspecifics (Racca et al., 2012). In line with this, dogs seeing a social stimulus typically associated with approaching behaviour have higher amplitude of tail-wagging movements to the right side reflecting prevalent activation of the left hemisphere, while the dogs seeing a social stimulus typically eliciting withdrawal response display higher amplitude of tail-wagging movements to the left side, implicating the right hemisphere (Quaranta et al., 2007). Further study based on cardiac activity and behaviour recordings demonstrated that dogs are able to detect tail-wagging asymmetry (Siniscalchi et al., 2013). A dog wagging the tail more to the left side elicit a greater emotional reaction in other dogs than a dog wagging its tail more to the right side.

Some theoretical (Rosa Salva et al., 2012) and empirical (Giljov et al., 2019) studies acknowledge the involvement of both brain hemispheres in social processing, avoid simplified dichotomous distinctions and argue that the relative contribution of two hemispheres depends on a set of motivational and emotional characteristics of the specific social response. This idea is supported by inconsistent empirical evidence unable to reject or clearly confirm any of the hypotheses about the relative hemispheric roles in social behaviour (e.g., Thomas et al., 2014; Prete et al., 2015). Most of the research in this area is based on experimentation while naturalistic investigations are scarce. A variety of social responses displayed by group-living mammals in their everyday activity can provide valuable insight into the lateralization of social brain. For example, observational field studies showed visual lateralization in agonistic interactions in feral horses in Australia (Austin and Rogers, 2012), Przewalski horses living under natural social conditions on a large reserve in France (Austin and Rogers, 2014), and free-ranging European fallow deer in Ireland (Jennings, 2012). These studies have provided new knowledge about the evolutionary origins of lateralization (Austin and Rogers, 2014) and fitness benefits associated with it (Jennings, 2012). Thus, an unobtrusive investigation conducted in a natural setting has proven to be an informative approach to the estimation of the hemispheric lateralization in real-life social situations (Karenina et al., 2017).

In the present study, we aimed to investigate visual lateralization in free-ranging European bison (*Bison bonasus*) in a variety of social contexts. Bison have laterally placed eyes and a small binocular overlap (Andreev, 1979) that enables to interpret one-sided preferences in their positioning relative to a stimulus as manifestations of hemispheric lateralization (Rogers, 2017). 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). To investigate diverse social responses of European bison they were observed in winter when these animals form large groups of mixed age and sex (Krasińska and Krasiński, 2013). One-visual field use prior to various social responses was recorded to test the association between the preferential use of the left/right visual field and the type of displayed social response.

2. Methods

2.1. Study site and subjects

The study was conducted on a free-ranging European bison (*Bison bonasus*) population in Orlovskoye Polesye National Park (53.27 °N 35.30 °E), Orel region, Russia. From 1996 to 2001, 65 European bison from different breeding facilities of the world were re-introduced in the national park which covers the largely forested area of 77000 ha within the species' former range (Geraskina et al., 2013). For the first time, the global gene pool of European bison was accumulated in a single population. From 1998 to 2016, 367 bison calves were born in Orlovskoye

Polesye NP (Geraskina et al., 2013). Currently, more than 500 bison inhabit unfenced woodland territories of the national park and adjacent areas of Kaluga and Bryansk regions (Karpachev and Prigoryanu, 2018). This Orel-Bryansk-Kaluga population of European bison is the second largest after the Bialowieza population and has unique genetic potential and prospects for further growth (Karpachev and Prigoryanu, 2018).

In summer, human involvement was limited to population monitoring, while in winter and spring, national park staff provided bison with supplementary food supply (wheat and hay). Food was dispersed by a single person on feeding grounds, large open areas surrounded by forest (former cattle pastures and fields). While in summer bison were highly vigilant, in the colder part of the year, the behaviour of bison towards people changed dramatically. The regular feeding grounds were visited not only by the staff providing forage but also by small groups of tourists and researchers. As a result, the sight of a human at the feeding place was well tolerated by bison.

2.2. Data collection

Observations were carried out on bison feeding grounds for 15 days in March 2018. Each of six feeding grounds was visited two or three times with the intervals of three days. Large woodless areas of feeding grounds provided clear visibility. There, bison formed large aggregations individuals that allowed observing various and frequent social responses. The data were collected by two observers standing in front of the hay barn, the place where bison most often saw humans prior to the study. Observers made an effort not to attract animals' attention by minimizing movements and noise. Dyadic interactions of European bison were recorded based on scan sampling method (Altman, 1974) for approximately 7 h per day. Data were recorded using pen and paper. Binoculars (12X magnification) were used if needed and social interactions were photographed whenever possible. Two observers continuously monitored different parts of the herd. Video recording was restricted by weather conditions and the short duration of the social responses, especially the subtle ones.

The methods of behavioural data scoring were generally similar to those used previously in the studies of lateralized social behaviour in young (Karenina et al., 2017; Karenina et al., 2018a; Karenina et al., 2018b; Giljov et al., 2018) and adult (e.g., Austin and Rogers, 2014; Farmer et al., 2018; Giljov et al., 2019) mammals with laterally placed eyes. The side placement of bison eyes makes it easy to distinguish whether one visual field or the other is being used with lateral head or whole body position relative to the conspecific as a proxy. One visual field used by the bison immediately before a social response was recorded. After one social response was scored, the observer switched her/his attention to a different location in an attempt to maximize the number of different individuals observed. Each individual was photographed after the social response was recorded. Only one social response per individual was included in the analyses (i.e. the bison included in the analyses of different categories of social responses were not the same individuals). The score was used only from the initiator of the given social response. The analysis based on single observations (responses) per individual is widely used for the estimation of population-level lateral biases (e.g., Coren, 1993; Forrester et al., 2014; Chapelain et al., 2015; Hill et al., 2017; Stor et al., 2019). Photo-identification based on natural markings or ear tags was used (Fig. S1) to exclude repeated observations of the same individuals.

2.3. Categories of social responses

Only the types of social responses clearly distinguishable by human observers and characterized by distinct lateral positioning of one individual relative to another were used in the analysis. Six categories of social responses were investigated.
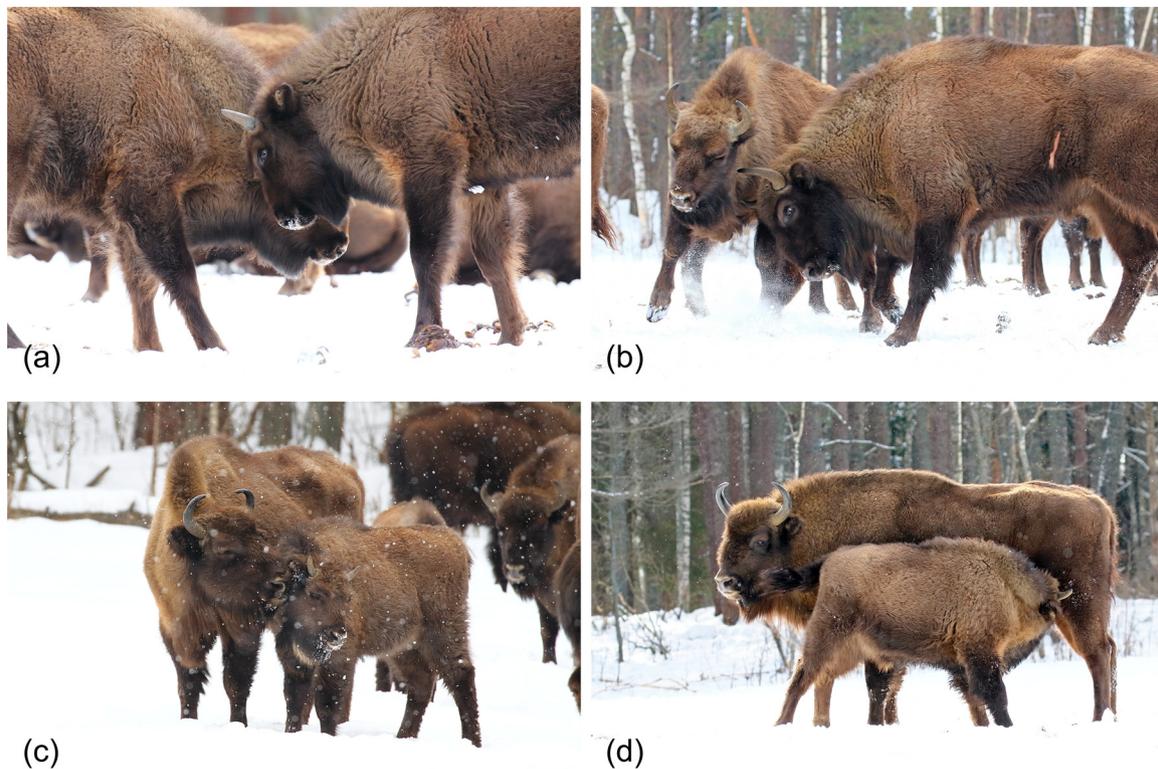
Fig. 1. Examples of social responses in which visual lateralization in bison was assessed, **(a)** fight, **(b)** side hit, **(c)** female-to-calf bonding, **(d)** suckling.

2.3.1. Fight

Two animals stood in front of each other, then one of the opponents put its head laterally to the other bison's head that resulted in both animals keeping the other in one visual field. If this lateral head positioning was immediately followed by a face-to-face fight with locking horns and head-butting, the response was recorded under this category (Fig. 1a). Only the response of the initiator of lateral head positioning was recorded. The fights observed did not reach escalated aggression typical for fights of rutting bulls (Krasińska and Krasiński, 2013).

2.3.2. Fight termination

After a face-to-face fight with locking horns and head-butting, one of the opponents put its head laterally to the other bison's head that resulted in a position similar to that in 'fight' category described above. In contrast to 'fight', the lateral head positioning was followed by both individuals terminating the fight and slowly turning away from each other.

2.3.3. Side hit

An animal turned its head to one side and hit the side of the body or head of another individual with one horn (Fig. 1b). This subtle form of aggressive/dominating behaviour was observed frequently and displayed in routine interactions between the individuals on the feeding grounds.

2.3.4. Female-to-calf bonding

A female turned its head to one side and started licking the side of the calf standing laterally relative to her (Fig. 1c). Licking is a typical component of maternal care in bison (Daleszczyk, 2004). There were no newborn calves in the bison groups during the period of the study, and licking was always brief and likely served for bonding rather than sanitary purposes.

2.3.5. Calf-to-female approach

A calf approached a female from behind when she is on the move and positioned itself on either her left or right side. The visual field the calf chose to keep the female was recorded. Only the approaches followed by the female and calf side-by-side joined movement for at least 30 s were included to discard incidental approaches when the calf just pass the female by when moving somewhere else. Despite being a forest dweller, European bison is follower species, with calves following their mothers from an early age (Daleszczyk, 2004).

2.3.6. Suckling

A calf approached a standing (or occasionally very slowly moving) female from the front, stopped near one of her sides and immediately started suckling (Fig. 1d). Only the approaches which resulted in the direct contact between the calf's mouth and female's udder area were included in the analysis.

The categories 1 and 2 were considered to be aggressive, while the categories 3–6 were classified as non-aggressive.

2.4. Data analysis

For each type of social responses, the significance of bias for bison using the left/ right visual field was tested using binomial z-scores. To estimate the difference in lateralization across responses, with aggressive and non-aggressive responses as subgroups, we also computed meta-analyses of proportions of lateral visual field use (Open Meta-Analyst software, Tufts University, USA; Wallace et al., 2012). Further analyses were conducted with the data on the responses not belonging to female – calf interactions. We examined whether the distribution of the left/right lateral visual field use was influenced by sex – age class of the bison the response was directed towards (female x male x juvenile x calf) using chi-square contingency table tests. Finally, the binary logistic regression model was used for the most common type of behaviour, *side hit*, to examine factors that influenced the odds to use the right visual field during a focal observation. The analysis was conducted using the JASP Statistical Analysis (ver. 0.9.0.1; https://jasp-stats.org/). All tests were two-tailed and significance level was set at

$p < 0.05$

2.5. 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 Orlovskoye Polesye National Park authorities. The study was purely observational. The behaviour of the researchers was similar to that of staff and tourists regularly visiting the feeding grounds that kept the disturbance of the bison to a minimum.

3. Results

In total, the analysis included social responses of 309 bison (one score per individual; see Supplementary Information for raw frequencies). Inter-rater reliability was assessed for the first 50 responses observed. The simple categorical coding of visual field use (left/right) performed independently by two raters was compared using kappa statistics, resulting in 96% reliability (kappa = 0.93, SE of kappa = 0.045; 95% C.I.: 0.85–1.00).

Analysis revealed a significant bias for using the right visual field prior to *fight* (38 out of 40 responses; $z = -5.53$, $p < 0.001$) and *side hit* (110 out of 157 responses; $z = -4.95$, $p < 0.001$). In contrast, bison used the left visual field significantly more often before *fight termination* (30 out of 32 responses; $z = 4.77$, $p < 0.001$). The chi-square test (4×2 contingency table) showed that the lateralization was not significantly influenced by the sex – age class of the bison the response was directed towards (χ^2 (3) = 2.55, p = 0.466).

The binary logistic regression model on *side hit* was performed and included laterality (the left/ right visual field use) as a dependent variable and sex and age class of the animal performing the response as fixed factors. The test of the model was found to be not significant ($p > 0.05$; see Supplementary Information).

In female – calf interactions, a significant bias for using the left visual field was found prior to all three types of responses: *calf-to-female approach* (21 out of 28 responses; $z = 2.46$, $p = 0.013$), *suckling* (26 out of 28 responses; $z = 4.35$, $p = 0.001$), and *female-to-calf bonding* (13 out of 17 responses; $z = 1.94$, $p = 0.049$).

The meta-analysis with aggressive and non-aggressive responses as two subgroups revealed that the aggressiveness of the responses significantly influenced the estimate. The pooled proportion of left visual field use was 0.88 in the non-aggressive responses (95% CI: 0.79, 0.96; $z = 7.22$, $p < 0.001$), and 0.17 in aggressive responses (95% CI: -0.07, 0.42; $z = -6.98$, $p < 0.001$). For four non-aggressive types of responses, the bias for the left visual field was found, whereas, for two types of aggressive responses, the right-visual field bias was evident (Fig. 2).

4. Discussion

Free-ranging European bison showed context-relevant visual biases for their social responses. The use of the left visual field preceded *fight termination*, *female-to-calf bonding*, *calf-to-female approach*, and *suckling* significantly more often than the right visual field use. While the recognition of emotional valence of animal behaviour in the wild can be speculative, it is reasonable to suggest that these responses represent non-aggressive forms of interactions. *Female-to-calf bonding*, *calf-to-female approach*, and *suckling* can be considered as positive. *Fight termination* is difficult to define as positive or negative; it is, however, associated with aggression inhibition, and i.e. belongs to non-aggressive type of responses. The oppositely-directed patterns of lateralization were found in two other categories of social responses. In most cases, bison kept the social partner in the right visual field prior *side hit* – a routine and subtle form of aggressive/dominating behaviour displayed frequently by different categories of individuals. Similarly, a more

active form of aggressive interactions such as *fight* was initiated more frequently when animals used the right visual field. Future study with a larger sample would enable assessment of individual preferences in bison social responses.

Thus, the bison were more likely to display aggressive responses when they viewed the conspecific with the right visual field, implicating the left brain hemisphere. In contrast, the responses associated with positive social interactions or aggression inhibition occurred more likely when the conspecific was viewed within the left visual field, indicating the advantage of the right hemisphere (Fig. 2). Somewhat consistent with these findings are the lateral biases reported for cattle, the most closely related mammal in which visual lateralization has been investigated (e.g., Robins and Phillips, 2010; Phillips et al., 2015; Robins et al., 2018). Cows that predominantly used their right eye in agonistic social encounters were more likely to dominate (Phillips et al., 2015). Together with the results of our study, this suggests that less fearful, combative behavioural patterns are controlled by the left hemisphere. By contrast, cows that predominantly used their left eye were more likely to submit in social encounters (Phillips et al., 2015). Thus, it can be assumed that in both cattle and bison, the right hemisphere predominantly controls responses requiring decreased aggression such as termination of or submission in agonistic encounters, and positive social contacts. Notably, the right hemisphere is assumed to be the dominant hemisphere for storing/learning information about social hierarchies including inferences about the individual's own status (Daisley et al., 2010). The greater probability of positive encounters and termination of aggression when the right hemisphere is in use may be explained by the improved evaluation of social hierarchy.

There is, however, little consistency between findings in bison and mammals more phylogenetically distant than cattle. Oppositely to bison, aggressive behaviour is under predominant control of the right hemisphere in a range of mammalian species (e.g., rat: Denenberg, 1981; dog: Racca et al., 2012; Siniscalchi et al., 2019; horse: Austin and Rogers, 2014; primate: Casperd and Dunbar, 1996). The evidence for the left hemisphere advantage for aggressive responses in bison doesn't support the assumption that the right hemisphere plays the dominant role in most aspects of social behaviour (e.g., Farmer et al., 2018; Forrester and Todd, 2018), but instead indicate the differential functions of both hemispheres. Furthermore, the direction of bison' visual biases is not consistent with the hypotheses purporting that the left hemisphere is dominant for positive emotions and approach, and the right hemisphere is dominant for negative emotions and withdrawal (Davidson, 1995; Najt et al., 2013; Kelley et al., 2017). The similar inconsistency has been found in the lateralized social behaviour of saiga antelope in the wild (Giljov et al., 2019). In saiga males, 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. Saiga calves showed the left visual field preference when approaching their mothers (Karenina et al., 2017). In two types of withdrawal responses studied in saiga males, left visual field bias was found for retreating after fighting, while no bias was evident in fight rejecting. Much like the results of the present study, this pattern of lateralized social responses does fit neither the right hemisphere dominance nor the positive–negative/approach–withdrawal distinction.

A number of human studies also failed to confirm any of the main hypotheses about lateralized social processing (e.g., Najt et al., 2013; Thomas et al., 2014; Prete et al., 2015). Thus, the cumulative evidence points to the fact that, in mammals, the relative roles of two brain hemispheres in the social behaviour are hardly explained by a simple, easily predictable pattern such as full dominance of one hemisphere or positive (approach) versus negative (withdrawal) distinction between the hemispheric roles. Lateralized social responses do not follow the similar pattern in different species, with oppositely directed biases observed in similar types of behaviour (e.g., aggression is predominantly controlled by the left hemisphere in bison, while it is
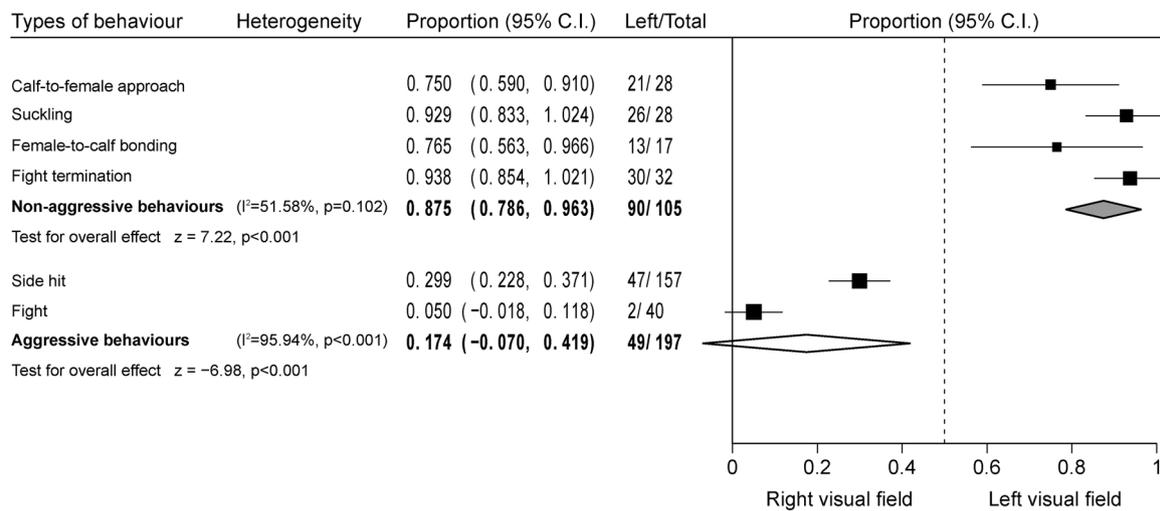
Types of behaviour	Heterogeneity	Proportion (95% C.I.)	Left/Total	Proportion (95% C.I.)
Calf-to-female approach		0.750 (0.590, 0.910)	21/28	
Suckling		0.929 (0.833, 1.024)	26/28	
Female-to-calf bonding		0.765 (0.563, 0.966)	13/17	
Fight termination		0.938 (0.854, 1.021)	30/32	
Non-aggressive behaviours	(I^2=51.58%, p=0.102)	**0.875 (0.786, 0.963)**	**90/105**	
Test for overall effect z = 7.22, p<0.001				
Side hit		0.299 (0.228, 0.371)	47/157	
Fight		0.050 (−0.018, 0.118)	2/40	
Aggressive behaviours	(I^2=95.94%, p<0.001)	**0.174 (−0.070, 0.419)**	**49/197**	
Test for overall effect z = −6.98, p<0.001				

Right visual field   Left visual field

Fig. 2. Forest plot of subgroup meta-analysis (random-effect) with aggressive and non-aggressive responses as subgroups. The proportion of left visual field use is shown for each type of social responses. Horizontal lines indicate 95% confidence intervals (CI) and rectangles reflect the point estimate. The diamonds reflect the pooled estimates across types of responses (white for aggressive and grey for non-aggressive responses). If the confidence interval does not cross the vertical dashed line (0.50), this implies that there is a significant difference between the lateralization observed and expected by chance only.

controlled by the right hemisphere in horse: Austin and Rogers, 2012, 2014). It seems that the division of social functions between the hemispheres is determined by a fine balance of emotions and motivations associated with the particular social behaviour. This hypothesis can explain conflicting results obtained in different species or research settings. Even the behaviours that are seemingly similar (e.g., they belong to a "positive" or "negative" category, as perceived by the human investigator) may have an unequal emotional and motivational background in different species or in the individuals of the same species under different circumstances.

Unlike other social responses studied, bison conformed to the general mammalian model in female – calf interactions (Karenina et al., 2017). Left visual field was used more frequently than the right in both females' responses directed toward the calf, such as bonding behaviour, and calves' behaviours towards the female, such as approaches and suckling. This is in line with the behavioural lateralization of mothers and offspring found in a wide range of terrestrial and aquatic mammals (Karenina and Giljov, 2018), as well as with the cradling bias in human females (Harris, 2010) and lateral preferences in human infants (Forrester et al., 2014). The remarkable interspecies consistency implies that mother – offspring relations are lateralized in a very conservative way in different mammalian species. This confirms the idea about an ancient evolutionary origin of lateralization in spatial mother – infant relations in mammals (Karenina et al., 2017).

Current knowledge suggests that behavioural lateralization is underpinned by selective advantages (e.g., Gunturkun et al., 2000; Vallortigara and Rogers, 2005; Dadda et al., 2010; Bell and Niven, 2016). In the context of the social processing, this implies that animals predominantly view the social stimulus with the visual field that provides the most appropriate and effective behavioural response which, in turn, provides better survival or mating success of the individual. Our work highlights the involvement of both brain hemispheres in the control of social behaviour with different hemispheres dominating in different aspects of behaviour. Future studies are required to test whether the preferential use of different visual fields (hemispheres) in different types of behaviours provide enhanced efficiency of these behaviours in an individual.

Declaration of Competing Interest

Authors have no competing interests to declare.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at https://doi.org/10.1016/j.beproc.2019.103959.

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