

Lateralization of mother–infant interactions in a diverse range of mammal species

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Left-cradling bias is a distinctive feature of maternal behaviour in humans and great apes, but its evolutionary origin remains unknown. In 11 species of marine and terrestrial mammal, we demonstrate consistent patterns of lateralization in mother–infant interactions, indicating right hemisphere dominance for social processing. In providing clear evidence that lateralized positioning is beneficial in mother–infant interactions, our results illustrate a significant impact of lateralization on individual fitness.

The preference to hold infants on the left rather than the right side of the body, as reported in human populations¹, reflects socio-emotional processes and potentially facilitates mother–infant relationships^{2–4}. Recent findings support the hypothesis that a left-cradling bias arises from the right hemisphere advantage for social processing^{5–7}, for example, visual recognition of infant facial expressions⁸. The position of an infant on the mother's left side may optimize maternal monitoring, by directing sensory information predominantly to the mother's right hemisphere^{3,9}. Right hemispheric superiority underlies the perceptual lateralization in social behaviours of many phylogenetically diverse taxa^{5,10}. More specifically, a variety of non-human mammals have shown a right hemisphere dominant role in the monitoring of conspecifics^{10,11}. Considerable evidence supports the idea that lateralized mother–infant interactions may not be restricted to the primate lineage. The paucity of studies on non-primate species restricts our understanding of how widespread and consistent lateralization is in mother–infant interactions among mammals. Here, we investigate the lateral biases in the behaviour of mothers and infants from a diverse range of mammal species.

Both mother and infant potentially impact on lateralization¹²; therefore, we aimed to differentiate their roles in asymmetrical positioning and to assess their lateral preferences separately. To record the choice of lateral position in mother–infant pairs, we studied 'follower-type' species, in which females and their dependent infants usually move side-by-side on parallel paths (Supplementary Fig. 1). Species with laterally placed eyes and relatively little binocular overlap were chosen because in such animals the expression of brain lateralization through one-sided behavioural biases is especially pronounced¹³. We employed a continuous focal animal sampling method¹⁴ to record spontaneous mother–infant reunions after short-term spatial separations. The choice of lateral position was recorded when one pair member approached the other from behind and positioned itself on either the left or the right side (see Methods for details). This sampling method allowed for a straightforward analysis of individual- and population-level lateralization

in a natural setting. Data consisted of 10,905 lateral position choices for 175 individually identified mother–infant pairs.

Hemispheric specialization for perception of conspecifics can be reflected by the physical positioning of individuals within their social environment^{15–18}. Therefore, a lateral position preference was used as a behavioural marker of social lateralization in infants and mothers. Infant lateral preferences at both the individual and population level were investigated in feral horses (*Equus ferus caballus*) living in natural social conditions and species living in the wild: Pacific walrus (*Odobenus rosmarus divergens*), Siberian tundra reindeer (*Rangifer tarandus sibiricus*), saiga antelope (*Saiga tatarica tatarica*), muskox (*Ovibos moschatus*), eastern grey kangaroo (*Macropus giganteus*) and red kangaroo (*M. rufus*). From one to five types of mother–infant behaviour were investigated for each species, with 'slow travelling' studied in all species. In slowly travelling pairs, the majority of infants (74–90%) preferred to keep mother on one side (left or right) rather than the other (Supplementary Table 1). Population-level analyses based on scores from an individual laterality index (see Methods) revealed a preference to keep mother on the left side, compared with the right side, in infants of all species (Fig. 1). An additional method of population-level lateralization testing that incorporates single observations per individual (see Methods) was used to increase the variety of studied species and behaviours. Based on this method, lateralization in an infant's position near the mother was investigated in wild argali (*Ovis ammon*) and southern right whales (*Eubalaena australis*).

A significant population-level bias for keeping mother on the left side was found regardless of the species, behavioural type (with only the exception of resting in reindeer, see Supplementary Tables 1 and 2), or type of analysis (multiple versus single observations). Importantly, a left-side bias existed in infants not only in routine behaviours, but also in stressful situations, such as when fleeing. Our results indicated that a lateral bias reflects the infants' preference to position the mother in their left hemisphere (left visual field) rather than the preference for a particular side of the mother's body. For example, Pacific walrus calves preferred to keep mother on the left side when resting both in a co-directed position ($z=2.16$, $P=0.029$) and in a counter-directed position ($z=3.06$, $P=0.002$) relative to the mother. That is, the leftward bias emerged regardless of which side of the mother's body was exposed to the infant. The same was true for foals and saiga calves showing a significant preference to keep mother on the left when approaching her for suckling from different sides of her body (see Supplementary Tables 1 and 2). Factors such as an infant's sex (tested in horses,

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grey kangaroos and red kangaroos) or age class (tested in walrus, horses and muskox) had no significant effect on lateralization (Supplementary Table 3).

The overall evidence for marine and terrestrial mammal species points to a common pattern of lateralization in an infant's perception of mother (Fig. 1, Supplementary Tables 4–12). A meta-analytic approach was used for interspecies comparison. First, the meta-analysis based on individual lateral preferences revealed a uniform infant preference to keep mother on the left side, as indicated in the forest plot (Supplementary Fig. 2). Second, the meta-analysis based on single observations per individual showed lateralized spatial positioning to be consistent between infants of 11 non-human mammals approaching mothers (overall meta estimate = 0.74, $P < 0.001$; Fig. 2) and for human children approaching adults¹⁵. Similar to mammals in the present study, human children have been investigated unobtrusively in a natural setting that facilitates comparison with our results. It is important to note that the control condition, that is, choosing a position relative to stationary inanimate objects, did not elicit any lateralization either in children¹⁵ or feral horse foals (see Supplementary Table 2). One-sided preferences in spatial positioning relative to a stimulus reflect the differential use of the lateral visual field of the left and right eye, and its underlying hemispheric specialization, as proved by a wide range of studies on vertebrates^{13,18,19}. Within this context, the spatial preferences demonstrated here arise from the dominant role of the right hemisphere in an infant's perception of mother. A left eye/right hemisphere advantage for the socio-emotional processing has been repeatedly reported for both human and non-human primates^{5,11}. For example, great apes preferentially keep conspecifics on their left side compared with their right side¹⁶, much like non-primate infants in the present study. Our findings support the theory that a right lateralized 'social brain' in primates, including humans, stems from earlier forms of lateralization common to vertebrates²⁰. The preference to keep a parent on the left side when begging for food observed in five out of six juvenile Australian magpies (*Gymnorhina tibicen*)²¹ may imply that the lateralization of parent–offspring interactions is not restricted to the mammalian lineage.

It is reasonable to suggest that a prevalent left-sided bias may confer advantages for an infant. To test this hypothesis, we analysed the behaviour of infants within the equal time intervals that they spent in different lateral positions (see Methods). First, we found that feral horse foals initiated more bonding behaviour (positive social contacts) with mother when they kept her on the left side, rather than the right side (paired t -test: $t_{18} = 4.97$, $P < 0.001$, $n = 19$). Second, we showed that the frequency of spatial separations between the pair members (when the infant was left behind the mother) was lower when the infant kept its mother on the left side before the separation, both in feral horses (paired t -test: $t_{19} = 3.65$, $P = 0.002$, $n = 20$) and Pacific walrus (paired t -test: $t_{10} = 6.25$, $P < 0.001$, $n = 11$). Thus, when perceiving a mother predominantly via the left eye–right hemisphere system, infants initiated more bonding behaviour and maintained the spatial proximity to mother more successfully than when perceiving her predominantly via the right eye–left hemisphere system (Supplementary Fig. 4). This may derive from a more general specialization of the right hemisphere for visuospatial processing, resulting in the attentional bias for the left visual hemifield²². Facilitation of bonding with mother and the maintenance of spatial proximity are obviously beneficial for an infant's survival²³. From the point of view of selective pressures, our findings indicate that it is advantageous for an infant to be left-lateralized.

We further demonstrate that the left-side bias in infants is not a specific response to mother, but derives from a more general lateralization in social behaviour. For example, all muskox calves studied showed individual preferences for a particular lateral position when approaching other familiar calves of the same age class ($z = 3.18$, $P < 0.001$, $n = 12$). A population-level preference to keep age mates

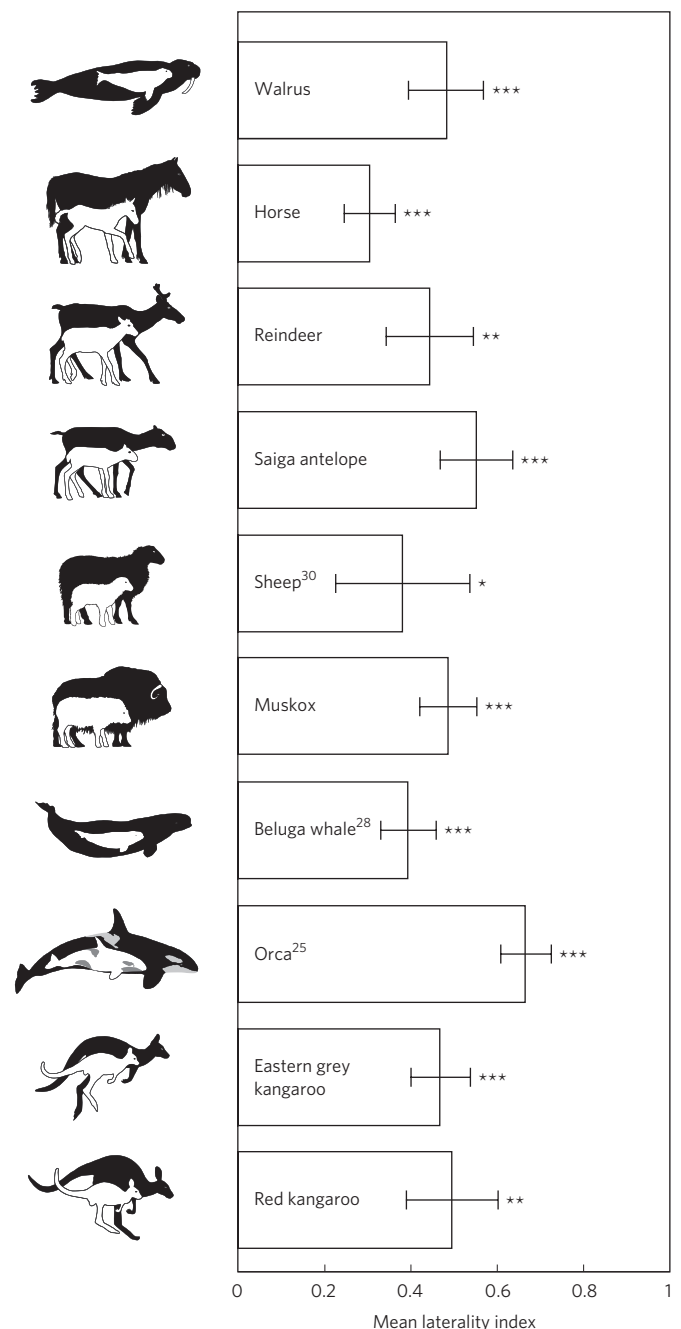


Figure 1 | Population-level preference for keeping mother on the left side in mammal infants. Mean laterality index scores based on multiple choices of lateral position from each individual infant (see Methods) are presented for Pacific walrus (Odobenidae; $n = 20$), horse (Equidae; $n = 24$), Siberian tundra reindeer (Cervidae; $n = 17$), saiga antelope (Bovidae; $n = 21$), domestic sheep³⁰ (Bovidae; $n = 31$), muskox (Bovidae; $n = 23$), beluga whale²⁸ (Monodontidae; $n = 23$), orca²⁵ (Delphinidae; $n = 7$), eastern grey kangaroo (Macropodidae; $n = 18$) and red kangaroo (Macropodidae; $n = 15$). The score for domestic sheep was calculated on experimental data from ref. ³⁰ for 3–6 month old lambs approaching their mothers. For all other species, the data on slow-travelling pairs were used. The data on argali and southern right whales are not presented because only single observations per individual were obtained for this species. Significantly positive values denote left-side bias. Error bars indicate the s.e.m. Population-level bias was tested using a one-sample Wilcoxon signed-rank test in all species except orca, in which a one-sample t -test was used. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$. See also Supplementary Table 1.

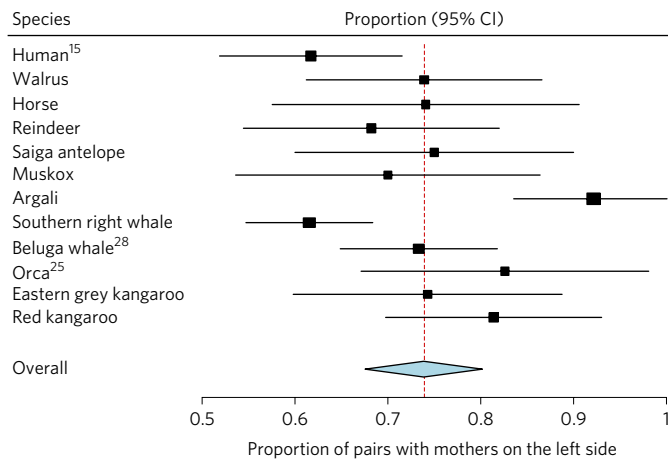


Figure 2 | Consistent lateralization of active choice of spatial position near the adult in 11 non-primate mammal infants and human children.

Forest plot for random-effect meta-analysis of proportions of lateral position choice by infants is shown. Analysis is based on the single choice of lateral position per individual (see Methods). Data on three species were taken from previous studies: human¹⁵, beluga whale²⁸ and orca²⁵. For human children (4 to 11 years old), data on approaching adults within a school playground ('M-Population' from ref. ¹⁵) were used. For each species, the proportion of infants, or children, who chose to keep the adult on the left side, is presented. Horizontal lines indicate individual 95% confidence intervals (CIs) and black boxes reflect the point estimate of individual species. The blue diamond reflects the pooled overall estimate (95% CI) across all species. The vertical red dashed line aids location of the pooled overall estimate relative to the individual species estimates. See Supplementary Fig. 3 and Supplementary Table 2 for the source data.

to the left rather than the right side was found ($W = 76$, $P < 0.001$). Analyses based on single observations per individual pair indicated similar left-side biases in infant–infant interactions of saiga antelope ($z = 2.59$, $P = 0.008$, $n = 18$), feral horses ($z = 2.18$, $P = 0.027$, $n = 29$), beluga²⁴ and orca²⁵. These results are consistent with the lateralization in human children when approaching a peer¹⁵. Lateral preferences in positioning towards conspecifics previously shown in interactions between adult mammals^{16,17} were found to occur also in interactions between immature individuals.

In contrast to the infants' lateral preferences, lateralization in a mother's choice of position was behaviour-type-specific (Supplementary Tables 13 and 14). In feral horses, the numbers of lateralized and non-lateralized mares were compared, with significantly more mares showing no side preference for slow travelling ($z = -2.62$, $P = 0.007$, $n = 21$) and resting ($z = -2.58$, $P = 0.007$, $n = 15$). No population-level biases were found in these behaviours (slow travelling: $W = -48$, $P = 0.383$; resting: $W = -59$, $P = 0.097$). Conversely, when fleeing, the majority of mares were lateralized ($z = 3.18$, $P < 0.001$, $n = 12$) with a population-level preference for keeping foals on the left side ($W = 76$, $P < 0.001$). A similar pattern was observed in wild eastern grey kangaroos. In slowly travelling pairs, the significant majority of females had no preference for a particular lateral position relative to an infant ($z = -2.02$, $P = 0.039$, $n = 12$), and there was no population-level bias (one-sample t -test: $t_{11} = 1.67$, $P = 0.123$, $n = 12$). However, analysis based on single observations per individual showed that, when fleeing, grey kangaroo mothers kept their infants predominantly on the left side ($z = 3.21$, $P < 0.001$, $n = 28$). Our results indicate that maternal lateralization was not pronounced in routine non-threatening circumstances, but emerged in stressful, potentially threatening situations. A left-sided bias has also been suggested for orca mothers when stressed by a vessel approach²⁵. We can assume that a left-side bias in mothers

is related to the increased need to monitor the infant in an unsafe environment. The left eye–right hemisphere system provides higher accuracy and speed for many types of social responses compared with the right eye–left hemisphere system^{5,10,18}. Therefore, when keeping an infant in the left visual field, the mother may derive optimal control of the infant state. This is generally consistent with human studies that have demonstrated that a left-cradling bias is most pronounced during the first weeks of an infant's life, when maternal visual monitoring of the infant's state is most critical⁶.

Our results demonstrate that humans are one of many species showing strongly lateralized mother–infant spatial relations. The remarkably consistent occurrence of lateralization in interactions between an infant and its mother indicate that this is likely to be a pervasive mammalian feature of ancient evolutionary origin. Previous studies have shown maternal lateralization for holding an infant^{1,6,26} in human and non-human primates. In this study we provide the first direct demonstration of lateralization in an infant's active choice of spatial position near the mother in a diverse range of mammal species. Our findings suggest that sensory lateralization facilitates mother–infant bonding. We empirically demonstrate the advantages of lateralized infant behaviour in both marine and terrestrial mammals in support of the hypothesis that lateralization contributes to biological fitness^{19,20,27}.

Methods

Data collection procedure. Data were collected in the course of 11 expeditions from 2012 to 2016. In addition, we analysed the photographs of southern right whales obtained during aerial surveys in 2005, 2008, 2010 and 2011. The data on beluga whales and orcas used here for interspecies comparisons were obtained during three expeditions from 2009 to 2011^{25,28}. The total number of subjects for each species varied according to the type of behaviour studied (see Supplementary Tables 1, 2 and 4–14). The study sites, observational conditions, total sample sizes and infant ages are given in the Supplementary Methods.

Observations with binoculars and video recording of animal behaviour were conducted for 5–9 hours per day during 37–62 days per species (with the exception of southern right whales, for which pre-existing aerial photographs were examined). Every effort was made to minimize any possible disturbance of animals during observations. After the animals were approached, we waited at least 10 minutes before beginning data collection. If the animal displayed a flight response, it was not chased. Observational conditions allowed for a reliable visual estimation of infants' sex only in feral horses, wild grey kangaroos and red kangaroos. Types of behaviour investigated in each species, and the photo-identification method used for recognition of individual pairs, are described in the Supplementary Methods.

We observed mother–infant pairs continuously and registered the choice of lateral position by pair members. The single choice of lateral position by an infant was defined as follows: after a pair member's spatial separation, the infant approached the mother from behind at a distance of less than one adult animal length, and then positioned itself on one side of the mother, that is, the infant chose a side-by-side parallel position relative to the mother. This was the most typical variant of mother–infant reunions, and all other variants were discarded from the analysis. The only exception was resting in a counter-directed position studied in Pacific walrus. In this case the infant approached the resting mother from the front, and then took a lateral position near her. Discrete responses were obtained as follows: after a single choice of lateral position was registered, a subsequent choice was taken into account only after the pair had separated by a distance of more than one adult animal length, when the infant again approached the mother from behind (or from the front in Pacific walrus when resting in a counter-directed position).

To ensure that the infant's choice of position was independent, we included only the events when the infant actively approached the mother, who moved forward or was motionless (depending on the type of behaviour investigated), and remained in an unbiased position (that is, the longitudinal axis of her body and head remained straight). If the mother turned her head or directed any other social response to the infant just before or during the infant's position choice (that is, before it took a lateral position), the event was excluded from the study. Mother–infant reunions from a focal pair were included in the analysis only when there were no other conspecifics within approximately five adult animal lengths. If any feature of the landscape could potentially prevent the infant from choosing one of the lateral positions (for example, there was a cliff, dense vegetation or the water's edge) on one side of the mother, such an event was discarded from the analysis.

The mother's choice of lateral position after approaching the infant from behind was investigated in feral horses and eastern grey kangaroos. A mother's lateral position choice was registered using the same inclusion criteria applied for an infant's choice. In muskox, saiga antelope and feral horses, the choice of lateral position in infant–infant interactions was scored using a similar method.

In further analyses for infants and mothers, we used a lateral position preference as a behavioural marker of lateralization. This non-invasive and unobtrusive approach has proved to be informative in assessing lateralized social behaviour in natural settings^{16,17,25,28,29}. The preference to keep conspecifics on one side of the body is widely accepted as a reflection of brain lateralization in social processing^{10,15,16}. Such interpretation of animal behaviour in a natural social environment is based on early experimental studies that have demonstrated that one-sided behavioural preferences are underpinned by hemispheric specialization^{19,20}.

In southern right whales, in contrast to other species studied, we analysed still images of mother–infant pairs. Images were selected that met the criteria as described previously²⁸ (see also Supplementary Methods for details).

Analysis of individual preferences. Preferences in lateral position choice were investigated in individual infants and mothers separately for each type of behaviour. Only the individuals with at least 15 position choice events were assessed for individual preferences.

The number of times an individual chose to keep the other pair member on the left side or on the right side was compared using a binomial test (z). As a result, each individual was classified as having no preference, or a preference for keeping the other pair member on the left/right side (Supplementary Tables 1 and 4–14). A binomial test was also used to examine the difference between the number of lateralized and non-lateralized individuals.

Analysis of population-level lateralization. The individual infants and mothers, for whom individual preferences were assessed, were included in population-level analyses. A widely applied laterality index (LI)^{15,25} was calculated for each individual using the formula $LI = (L - R) / (L + R)$, where L and R are the number of times the individual chose to keep the other pair member on the left or right side, respectively. LI scores range on a continuum from -1.0 to 1.0 , with negative values indicating the right-side bias and positive values indicating the left-side bias. According to a Shapiro–Wilks test, the data were not normally distributed, therefore nonparametric tests were used. A one-sample Wilcoxon signed-rank test (W) was applied to evaluate the significance of population-level bias. All tests in the study were two-tailed and the level of significance was set at 0.05 .

Besides the population-level analyses based on multiple observations (≥ 15) of focal individuals, we conducted analyses based on single observations per individual (see Supplementary Methods for details). The first observation of lateral position choice from each individual was included in the analysis. This method was used to enhance comparability of data across studies (for example, to compare our data with data on human children¹⁵), and to increase the variety of studied species and behaviours. In argali and southern right whales, the analysis of single observations per individual pair was the only method of population-level analysis.

The consistency of lateralization across species was estimated using a meta-analytic approach. Random-effect subgroup meta-analysis (with each species as a subgroup) for multiple observations on focal individuals and random-effect meta-analysis for single observations per individual were computed using Open Meta-Analyst software, Tufts University, USA.

Estimating the advantages of lateralization. Here we aimed to exclude the influence of the infant's preference for a particular lateral position. Therefore, in the analysis, the time intervals that infants spent keeping mother on the left and right side were equal. For each infant, in each day of observations, such intervals were equal to the least amount of time the infant spent keeping the mother on either side. First, we investigated the frequency of bonding behaviour initiation by feral horse foals in different lateral positions. Bonding behaviour was defined as positive social contacts easily recognizable by the observer, such as grooming (soft nibbling with teeth) and rubbing with the head or lips only²³. Second, the frequency of spatial separations between the pair members was investigated. In feral horses and Pacific walrus, we analysed situations when the pair members travelled slowly side-by-side until the mother kept moving forward, while the infant was left behind her at an approximate distance of 10 m or more. We included in the analysis only the situation when the infant was alarmed after the spatial separation²³ and tried to rejoin the mother, that is, the infant most likely did not leave the mother intentionally. Finally, we tested whether the frequency of both types of event (spatial separations and initiation of bonding behaviour) differed significantly between two lateral positions (when the foals kept their mother on the left or the right side). Parametric paired t -tests were conducted as the data were normally distributed (Shapiro–Wilks test).

Data availability. The data supporting the findings of the study are available within the article and its Supplementary Information.

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Author contributions

K.K. and A.G. designed the study, organized the expeditions, performed data collection and analyses, and wrote the paper. J.I. helped to organize the field work and to collect data on grey kangaroos, and contributed to and edited the paper. V.R. performed the individual identification of southern right whales and edited the paper. Y.M. supervised the project, collected data, and contributed to and edited the paper.

Additional information

Supplementary information is available for this paper.

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Competing interests

The authors declare no competing financial interests.