Behavioural lateralisation in reindeer

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Abstract: Reindeer (*Rangifer tarandus*) kept in corrals or otherwise forced to clump typically start milling in response to stressing events. This behaviour is generally considered to have an antipredator effect. An inquiry on herd behaviour, to which 35 Norwegian reindeer husbandry districts responded, showed that 32 experienced that corralled reindeer consistently circled leftwards, whereas the remaining three reported consistently rightward circling. Regular monitoring of a reindeer herd in central Norway over a two-year period (1993-94), and experimental studies on a fraction of the same herd, revealed the following traits. Free-ranging reindeer showed no right- or left-turning preference during grazing or browsing, but when the reindeer were driven into corrals or forced to clump in the open they invariably rotated leftwards. The circling of corralled reindeer was triggered at an average group size of 20 to 25 animals, apparently independently of the age and sex of the animals. When they dug craters in the snow to reach food, the reindeer used their left foreleg significantly more often than their right. In 23 out of 35 reindeer, the right hemisphere of the brain was heavier than the left. However, in the sample as a whole, the weights of the left and right hemispheres did not differ significantly. Lateralised behaviour in reindeer is thought to be determined by natural and stress induced asymmetries in brain structure and hormonal activity. In addition, learning is probably important for passing on the behaviour between herd members and generations. Differences in lateralised behaviour between nearby herds are thought to be related primarily to different exposure to stress and learning, whereas genetical and environmental factors (e.g. diet), age structure and sex ratio are probably more important for explaining differences between distant populations.

Key words: asymmetry, circling, footedness, left/right dominance, *Rangifer tarandus*, rotation.

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Introduction

Although man seems to have a tendency to look upon nature as mainly symmetrical, a closer look at anatomical, morphological, behavioural and other features in animals and plants indicates that asymmetry may be the rule rather than the exception. Probably the most cited expression of asymmetry is the occurrence of sinistrality and dextrality in man (see review in Bradshaw & Rogers, 1993). Lateral biases in handedness are also found in nonhuman primates (e.g. McGrew & Marchant, 1997; Singer & Schwibbe, 1999), and preferences in the use of the right and left feet and paws have been convincingly demonstrated in rats and mice (Bradshaw & Rogers, op. cit.), dogs (e.g. Tan, 1987), cats (e.g. Pike & Maitland, 1997) and birds (e.g. Rogers & Workman, 1993). Furthermore, Thing (1977) reported that wild caribou *Rangifer tarandus* in Alaska tended to use their right forelegs slightly more than their left ones when digging craters in

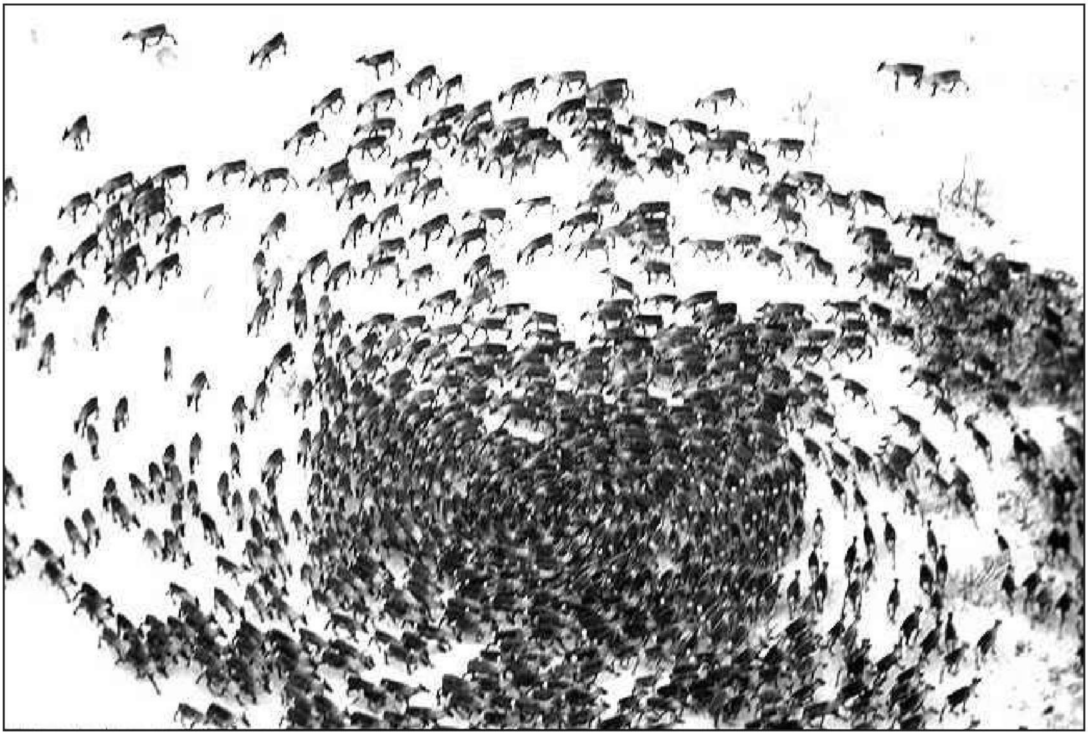

Fig. 1. Free-ranging reindeer herd circling counterclockwise. Photo courtesy of Jon J. Meli.

the snow while foraging. However, a similar study on foraging muskox *Ovibos moschatus* did not reveal significant biases in footedness, on either the individual or population levels (Schaefer & Messier, 1997).

Another form of behavioural lateralisation is the turning and rotating biases found in many animals. Thus, when moving under free-field conditions both humans and rats tend to turn rightwards (Glick & Cox, 1978; Bracha *et al.*, 1987; Mead & Hampson, 1996), as do hamsters in an experimental arena (Uziel *et al.*, 1996), whereas counterclockwise turning predominates in swimming dolphins *Tursiops truncatus* (Sobel *et al.*, 1994), grazing caribou (Pruitt, 1960) and possibly in impalas *Aepyceros melampus* (Jarman, 1972). Evidence for individual preferences in turning direction has been recorded in teleost fish escaping from predators (Bisazza *et al.*, 1997), as well as in several domestic animals, such as goats (Ganskopp, 1995; Hosoi *et al.*, 1995a), sheep (Hansen *et al.*, 1978; Lynch *et al.*, 1992; Hosoi *et al.* 1995a), cattle (Hosoi *et al.*, 1995b) and horses (Espach *et al.*, 1993; Grandin, 1993).

In humans and most other vertebrates, the two hemispheres of the brain differ in size (the right side normally being larger than the left) and function (see reviews in Walker (1980) and Bradshaw & Rogers (1993)). There is ample evidence for a close connection between these brain asymmetries and various expressions of behavioural lateralisation, though exceptions are reported (e.g. Tan & Çaliskan, 1987). Furthermore, it is commonly accepted that lateralisation develops in response to the interactions between genetical, environmental and hormonal factors (Bradshaw & Rogers, 1993). Numerous authors (reviewed in Bradshaw & Rogers, op. cit.; Cabib *et al.*, 1995) have reported on the relationship between asymmetry in the concentration of the neurotransmitter dopamine in the brain and the preferential handed-/footedness and the lateral biases in turning and circling behaviour recorded in many animal species.

Although rarely documented in the scientific literature, it is widely recognised in reindeer husbandry that when groups of reindeer (*Rangifer tarandus*) are kept in corrals for handling (e.g. sorting, slaughtering, marking, etc.) or otherwise forced to clump (e.g. when stressed by potential predators and harassing insects), the whole group may start circling, usually leftwards (Fig. 1). This behaviour is reported to be characteristic of both domestic (N. Kuhmunen, unpubl.; L. Baskin, pers. comm.) and wild reindeer (Lier-Hansen, 1994; Skogland, 1994), and Pruitt (1960) reported that migrating bands of caribou tended to drift to their left as they fed along their route. Although counterclockwise thus appears to be the predominant turning direction in reindeer/caribou over most of their range, clockwise rotation has occasionally been reported, although not documented, to be the rule in some Scandinavian reindeer herds.

The aim of this study, which was conducted in 1993 and 1994, was to provide documentation of the occurrence of lateral asymmetries in domestic reindeer, primarily the reported predominance of left-handed circling, and basic information for explaining this lateral bias. In addition, we also investigated laterality in footedness in foraging reindeer. The relative frequencies of right- and leftward rotating herds in different parts of the Norwegian reindeer husbandry region were investigated, as well as the frequency of individual differences in a single herd and the persistence of the behaviour over time. Field experiments were also made to investigate the possible importance of age, sex and group size for the circling behaviour, and the possible relationship between lateral behaviours and brain asymmetry was also examined.

Material and methods

Inquiries and observations in corrals

In order to investigate the frequency of left- and rightward circling herds and their regional distribution in Norway, the local administrators of reindeer husbandry districts were asked to report on the behaviour in the various herds in response to various handling procedures. Thus, reports on the usual circling direction observed, the approximate number of animals and the type of handling were received from 35 herds located in the four northernmost counties and the reindeer husbandry districts of southern Norway.

The stability of the circling behaviour over time was investigated by repeatedly observing herds of corralled reindeer in the Østre Namdal reindeer husbandry district in the county of Nord-Trøndelag. Thus, over a period of two years, the behaviour of reindeer herds corralled at different places for marking, sorting, slaughtering, etc., was recorded on 10 occasions during autumn, winter and spring. The size of the herds varied from 70 to approximately 4000 animals.

Field observations

Possible left and right asymmetries in the moving and turning directions of free-ranging, grazing reindeer were recorded under both summer and winter conditions by counting the number of left and right turnings in each of 41 focal animals (34 adult females and 7 calves) sampled from a herd of approximately 4000 animals. The length of observation time per animal varied depending on the varying possibilities for keeping the animals in sight. In addition, five adult females were equipped with radio transmitters, mounted on collars, which enabled us to plot the positions of the animals at regular intervals on a map on the scale of 1:50 000. The number of recordings per animal varied from 4 to 37, with a mean of 15.0 recordings.

Possible asymmetries in footedness in the reindeer were investigated by recording their use of the left and right forelegs when digging foraging craters in the snow. For each of 29 animals (3 adult males, 25 adult females and one calf), randomly selected from the above-mentioned 4000-strong herd, the number of digging movements performed by each of the forelegs during five minutes was recorded. The number varied from 15 to 160, with a mean of 61 movements. A total of 1772 digging movements were recorded.

Experiments

Test arena and experimental design.

A test arena was established in connection with one of the main corrals in the Østre Namdal reindeer husbandry district in Nord-Trøndelag (Fig. 2). The arena consisted of a Y-shaped entrance connected at one end to the main corral and a small «waiting» corral, and at the other end to a test corral. A 1.6 m

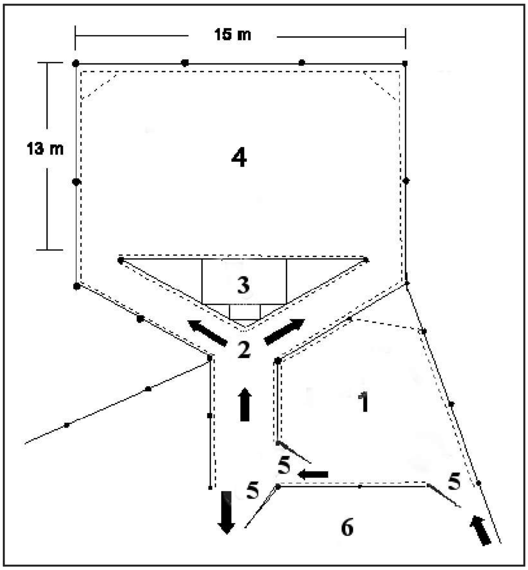

Fig. 2. Test arena used in the field experiments.
1. «waiting» corral, 2. Y-entrance, 3. observation tower, 4. test corral, 5. gates, 6. main corral. Wire-netting fences (•—•—•) and covering (.......) were used for screening.

high observation tower was placed in the centre of the arena. The test corral and the «waiting» corral, as well as the Y-entrance and the observation tower, were screened from outside by a 1.6 m high wire-netting fence and a 2 m high, non-transparent sackcloth.

Animals participating in the experiments were driven from the main herd into the «waiting» corral where they were allowed to calm down for some time before the experiments started. When they entered the test corral, the animals had to pass through the Y-entrance, and whether they chose the left or right branch was recorded. In the test corral, the experimental groups, which varied with respect to the number, sex and age of the animals, were observed and their spontaneous moving direction was recorded at certain intervals. A varying number of animals was used for the different experiments. In all, 116 animals were used, 26 adults and 90 calves. The adults, which were individually marked with numbered plastic collars, were made up of equal numbers of males and females. All the experiments were performed in December.

Testing the role of the number, age and sex of the animals.
The number of animals required to attain spontaneous, consistent circling was investigated in a series of five experiments by driving one, two or three animals at a time into the test corral until the number was reached at which circling was assessed to be synchronous and unilaterally stable. The experiments involved 72 calves and 58 adult reindeer of both sexes, some of which were used in two or more experiments.

To investigate whether the required group size for attaining spontaneous, stable circling was related to the age of the animals, three experiments were performed with calves alone. The animals were driven into the test corral until a group of five had gathered. The behaviour of the calves, i.e. whether they stood inactive or moved in either direction, was then observed and recorded for 1 min. If the group did not start circling, another group of five calves was let in, and the behaviour of the now 10 calves was observed and recorded as described for the first group. This procedure was repeated until a spontaneous, stable circling behaviour was shown. The experiments involved 70 different calves.

The role of sex for the establishment of a spontaneous, stable circling behaviour was investigated in three experiments with each of the sexes. An adult female or male was let into the test corral together with two calves. The behaviour of the animals, i.e. whether they stood inactive or moved in either direction, was then observed and recorded for 1 min. Then another group of one adult and two calves was added, and the behaviour of this enlargened group was recorded in the same manner. The procedure was repeated until spontaneous, lateral circling took place. The six experiments performed involved 20 adults of each sex and 40 different calves. Some of the adults were used in two or more experiments.

Brain measurements
Possible asymmetries in the brain were investigated by weighing the left and right hemispheres of 35 reindeer culled during November to March. Twenty-nine were adult females, five were adult males, and one was a nine-month old calf, and all came from the same herd as was used for both kinds of behavioural study. After the brains had been removed from the skulls, they were fixed and stored in 4% formalin for 6 months. The cerebellum and medulla were then removed and the two hemispheres were separated through corpus callosum. Before they were weighed, the hemispheres were dehydrated for 2 weeks in concentrated ethyl alcohol. The hemispheres were weighed to the nearest 0.1 gram.

Statistical analyses
Data analyses were conducted using the software package SPSS/PC 8.0. All P values are two-tailed, statistical significance was accepted at the $\alpha = 0.05$ level, and means are given with ± standard error of the mean (SEM).

Results

Inquiries and observations in corrals
The local offices managing reindeer husbandry were asked for information about the direction in which temporarily corralled herds circled. Of the 35 (31%) responses received, 32 reported that corralled herds in their district invariably circled in a leftward direction. The other three districts (one in Finnmark and two in Troms) reported that they always circled in a rightward direction. The behaviour of approximately 600 animals from the rightward-circling herd in Finnmark was also recorded on video tape.

Repeated observations over a two-year period of reindeer periodically fenced in for various reasons revealed that the animals always maintained a leftward-circling behaviour throughout the period concerned, irrespective of season, location and type of handling. Furthermore, a similarly biased milling behaviour was recorded on two occasions under unfenced conditions when groups of reindeer were driven together on ice-covered lakes.

Field observations

In a monitored sample of grazing and browsing reindeer numbering 39 adult females and 7 calves, neither individuals nor groups showed significant preferences for turning right or left when moving around under natural, undisturbed conditions. Thus, 18 showed leftward-dominated turnings, 18 turned more often to the right, and 10 equally often turned right and left. Furthermore, of the 695 turnings recorded in the sample, 354 (50.9%) were to the right and 341 (49.1%) to the left (Wilcoxon signed ranks test, z=-0.650, P = 0.516). Nor was there any significant difference between the adult females and the calves with respect to turning preferences (Fisher's Exact test, P = 0.338).

When digging foraging craters in the snow, all the 29 monitored reindeer used both their forelegs, although the left/right dominance varied significantly between individuals, 21 most frequently using their left foreleg and eight their right (Sign test, z=-2.228, P=0.026). Analyses of the 1774 recorded digging movements showed that 1011 (57.0%) were performed by the left and 763 (43.0%) by the right foreleg, which is significantly different from a random distribution (Wilcoxon signed ranks test, z=-2.109, P=0.035). Although there were only three males in the sample, there was no indication of sex differences in «footedness» (Fisher's Exact test, P=0.536).

Experiments

Left/right choice in the Y-entrance.

Records were kept of whether animals entering the test corral for the first time chose the left or right branch of the Y-entrance. Of the 116 animals used in this experiment, 84 preferred to enter from the left, which is significantly more than would be expected if both branches were chosen with the same probability (Sign. test, z=- 4.735, P<0.001). On subsequent occasions, the animals invariably chose the left branch. Side preference did not differ significantly between adults and calves (c^2=1.17, df=1, P=0.279), or males and females (Fisher's Exact test, P=0.141).

The role of group size, age and sex.

Single reindeer and groups made up of a few animals did not show a spontaneous and consistent circling behaviour in the test corral. However, when the number in the group was gradually increased, a level was finally reached at which circling, invariably leftward, was spontaneous and consistent. In five experimental groups, in which the animals were mixed with respect to age and sex, this level was reached when the group numbered 21, 21, 22, 28 and 38 animals, respectively (mean=26±3.3). Similarly, in pure calf groups (n=3), unilateral leftward circling was established at 25, 25 and 20 animals, respectively (mean=23.3±1.7). When calves were added to female and male groups (n=3 for each sex), spontaneous and invariably leftward circling was established at 18, 18 and 24 animals (mean=20±2.0) and 18, 21 and 21 animals (mean=20±1.0), respectively. The mean number of animals in the different types of experimental groups did not differ significantly (ANOVA, $F_{3,10}$=1.267, P=0.338), indicating that the group size required for circling to be triggered is independent of the age and sex of the animals.

Brain laterality

There was a strong tendency (23 of the 35 animals examined) for the animals to have a heavier right brain hemisphere than left (Sign test, z=-1.69, P=0.091). However, in the sample as a whole, there was no significant difference between the mean weights of the two halves of the brain (right: 65.±1.4 g, left: 64.9±1.3 g, Wilcoxon signed ranks test, z=-1.294, P=0.196). Nor was there any evidence that males and females differed with respect to brain asymmetry (Fisher's Exact test, P=0.635).

Discussion

There are numerous examples that animals belonging to a variety of social and aggregating species actively decrease the distances to each other and form more or less tight groups when threatened by predators, harassed by insects, or otherwise subjected to stressing, external stimuli. By avoiding being at the periphery of the group, but instead seeking a more central position and being closely surrounded by as many neighbours as possible, this behaviour is generally believed to decrease the likelihood of a specific individual being at serious risk (for a review of group living, see e.g. Alcock, 1998). Both domestic and wild reindeer (with the exception of the Svalbard reindeer, *R. t. platyrhyncus*) are, like many other social ungulates, known for their readiness to form very tight groups when subjected to outside disturbances, and this behaviour is generally considered to have developed in response to heavy predatory pressure in a landscape with limited possibilities for individuals to find cover (Bergerud, 1974). Unprotected animals in the periphery of the flock are likely to be subjected to heavier attacks from predators (Cumming, 1975) and parasitising insects (Espmark, 1968) than those in a more central position, which are strongly protected physically by the mere nearness of other animals. Furthermore, the endeavour by individual reindeer to attain an inner position in the group makes the animals change their positions almost incessantly, and this, in combination with the strong tendency in reindeer to behave synchronously, may lead to a rotational movement by the entire group. In addition to being physically protected by the mere nearness of other animals, the individual members of a milling herd are thought to gain protection from attacks from predators by the dilution effect and by confusion due to swarming (Cumming, 1975). The observation in this study that consistent rotation was triggered at a group size of approximately 20 to 25 animals suggests that the dynamics of the group are related to the number of animals, i.e. the amount of restlessness and the intensity of excitement have to reach a certain level before circling is triggered.

However, although these mechanisms may explain the background for circling, they do not explain why reindeer consistently rotate in one direction, usually leftwards. In many species, the direction of turning and rotational movements is commonly consistently biased at the group level, although individual preferences have been shown to be typical for many species (e.g. Carlson & Glick, 1989; Sobel *et al.*, 1994; Ganskopp, 1995; Uziel *et al.*, 1996; Bisazza *et al.* 1997). Furthermore, turning preferences in the open field tend to be consistent with circling biases in confinement. Thus, although not confirmed by this study, Pruitt (1960) reported that free-ranging caribou tended to turn leftwards as they moved when foraging, i.e. biased in the same direction as recorded in the confined reindeer in this study. However, both humans and dolphins are reported to have a tendency to turn towards the right when moving in free field, while they preferentially rotate leftwards in confinement (Bradshaw & Rogers, 1993; Sobel *et al.*, 1994). It has been speculated that these apparently contradictory tendencies are due to the fact that on entering a confined area, a right-turning subject will encounter a barrier (wall, fence, etc.) to the right and thus have to turn left when moving on (Bradshaw & Rogers, 1993). However, this possibility does not apply to the reindeer in this study. Although the animals did not show any particular turning biases under free movement, they were significantly left biased on entering the test corral, and this bias was invariably maintained during circling.

This study has clearly demonstrated that counterclockwise circling in groups of stressed reindeer is a common and consistent feature in most of the Norwegian reindeer husbandry region. Furthermore, the behaviour is maintained persistently over time and seems to be independent of season, locality and type of stressing event. However, there are exceptions to this general pattern. Thus, a few scattered herds, especially in the north, are just as consistently right biased in their circling behaviour, notwithstanding the fact that neighbouring herds are usually left biased. To help to explain this puzzling condition, as well as the reindeer's unidirectional rotating behaviour in general, a brief outline of the controlling processes behind behavioural lateralisation in mammals would be appropriate. Most of our current knowledge is based on comprehensive studies of rats and mice (reviewed in Bradshaw & Rogers, 1993) and, although these species have come to be accepted as fairly typical for nonprimate mammals, specific features may vary between species or groups of species.

From a proximate point of view, any form of behavioural asymmetry in individuals and populations is determined by interactions of genetic, environmental and hormonal factors. Genetic factors may specify the strength of lateralisation, but are probably not able to influence its direction, i.e. whether an individual or a population is right or left biased in circling or footedness (Collins, 1985). Environmental factors, such as diet, social conditions and stress as a result of, for instance, handling procedures, are known to have an influence on the hormone levels in the brain. Varying hormone levels may themselves influence the strength and direction of lateralised behaviour and, in addition, may contribute to the development of structural and functional brain asymmetries. Thus, most species investigated so far have been shown to have asymmetrical brain structures, and the right hemisphere, which controls spatial abilities such as the turning direction, is usually larger than the left. Likewise, asymmetries in the dopamine activity in various basal ganglia structures have been found in many species, and this asymmetry, like that in the activity of other hormones and size-biased brain structures, is closely associated with different forms of lateralised behaviour. Thus, circling direction and footedness in individual rats is to the side ipsilateral to the lower level of dopaminergic activity, and right-biased behaviour in, for example, cats, dogs, rabbits, whales and dolphins is often associated with right-dominated hemispheres. Internal and external environmental stimulation is known to cause structural and hormonal changes in the brain of developing individuals, and may strongly influence the development of lateral behavioural asymmetries. However, although brain plasticity is largely a property of the developing brain, very much of this plasticity is retained into adulthood, which means that even the adult brain is able to adapt to changing environmental and hormonal conditions, and this is likely to be an important background for variations in behavioural asymmetries between individuals and populations. Furthermore, studies on mice have shown that individuals can learn lateralised behaviours simply by observing other animals (Collins, 1988).

These results, although largely obtained in studies on mice and rats, suggest that the unidirectional rotating behaviour in reindeer is related to hormonal and structural asymmetries in the brain, and that the default asymmetries are associated with leftward circling. Different circling preferences between neighbouring herds could possibly be related to genetical and environmental factors such as food, as well as to the age and sex structure in the herds, but differences between the herds in these respects are thought to be small and of limited, if any, importance in this context. However, probably a more likely explanation is associated with differences in handling procedures and intensity. Handling is generally considered to be stressful to the animals and is likely to cause hormonal changes that affect brain laterality and stimulate asymmetric dopaminergic activity in the brain, which again influences the lateralisation of the behaviour. Thus, increasing hormonal activity in the brain due to intense and frequent stressful events, in utero or later in life, may alter the structural and hormonal asymmetry in the brain thereby influencing the direction of the behavioural asymmetries. The same argument may also apply with respect to the observed individual differences in footedness in connection with the digging of foraging craters, although genetical and possible environmental differences (e.g. diet) may be more important for explaining the observed differences in footedness between reindeer and Alaskan caribou (Thing, 1977). Furthermore, a reindeer herd is typically characterised by its members imitating each others behaviour, and if some animals become biased in one or another direction with respect to circling or footedness, this may spread to the rest of the group by copying. The observed persistency in circling behaviour in reindeer over time, irrespective of season and other environmental factors and involving all age classes, is consistent with the possibility that learning is important in maintaining the behaviour and in passing it on from generation to generation.

Several studies, including not only rats and mice but also other nonprimate mammals, primates and birds, have demonstrated the role of sex hormones for the development of lateral asymmetries (reviewed in Bradshaw & Rogers, 1993). Thus, differences between males and females and between young and adults with respect to turning/circling preferences and handedness/footedness have been amply documented. With respect to reindeer, Espmark (1977) reported that adult animals preferably used their right hindleg when performing the hindleg-head contact behaviour, whereas juveniles and calves tended to be left biased. In modern reindeer husbandry, the sex ratio is strongly skewed in favour of fertile females, and heavy culling of «superannuated» animals and calves distorts a natural age distribution. These skewnesses in population structure probably apply to most of the domestic reindeer herds in Norway, and are thus not likely to be important for the observed differences in laterality between herds. However, age and sex biases in reindeer herds, in addition to possible genetical and environmental differences, may be more important for explaining the observed differences between reindeer and caribou with respect to footedness (Thing, 1977) and possibly also with respect to turning preferences (Pruitt, 1960).

Although the overall mean weights of the right and left hemispheres of the brain did not differ significantly, there was a strong tendency in this study for a heavier right hemisphere in most of the reindeer. This is consistent with the findings in several other species (reviewed in Bradshaw & Rogers, 1993). The fact that most of the reindeer had right-biased brains and that the herd from which the brains were sampled was characterised by leftward rotation and significantly left biased with respect to foreleg use in crater digging, is consistent with earlier findings that brain asymmetry is associated with behavioural lateralisation (reviewed in Bradshaw & Rogers, 1993), although other studies (e.g. Tan & Çaliskan, 1987) have found no correlation between asymmetries in hemisphere size and behavioural side preferences.

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