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Relationship between Motor Laterality and Aggressive Behavior in Sheepdogs

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Received: 10 January 2019; Accepted: 11 February 2019; Published: 15 February 2019

Abstract: Sheepdogs' visuospatial abilities, their control of prey-driven behavior and their motor functions are essential characteristics for success in sheepdog trials. We investigated the influence of laterality on 15 sheepdogs' (*Canis familiaris*) spontaneous turning motor pattern around a herd and on their behavior during the first encounter with sheep in a training session. The most relevant finding of this research was that the dogs displayed significantly more aggressive behavior toward the sheep when turning in a counterclockwise direction around the herd. Considering that in counterclockwise turns the sheep were in the dogs' left visual hemifield, the high frequency of aggressions registered during counterclockwise turns suggests right hemisphere main activation. Overall, our results revealed the existence of a relationship between motor lateralization and aggressive behavior in dogs during sheepdog training and have practical implications for sheepdog training.

Keywords: dog; behavior; laterality; vision; physiology

1. Introduction

Sheepdog trials are a worldwide sports competition involving dogs and handlers, in which the dogs' ability to manage sheep properly during different daily working activities is tested (e.g., gathering, driving, shedding, penning, and singling). Historically, sheepdogs belong to different breeds, which were selected to cooperate with humans in sheep raising, specifically in guarding and herding the animals [1]. As a consequence, the selection and training of dogs are fundamental aspects for both farm work and sheepdog trials. Among the required characteristics, the visuospatial abilities of the dogs and their control of their motor functions and prey-driven behavior are essential for the success of sheepdog activities. Predatory aggressive behavior is a part of the predation functional system, which includes different behaviors aimed at capturing and killing the prey. According to the definition of aggression, animals display aggression with the intention to do harm. Therefore, predatory aggressive behavior falls into this category, even though the animal's motivation is very different from that in other forms of aggression (e.g., social aggression) [2].

There is now clear evidence that visuospatial information is analyzed in an asymmetrical way by the dogs' brains and that it is associated with asymmetries of the dogs' motor functions [3,4]. Specifically, it has been found that agility-trained dogs displayed longer latencies to complete the weave pole obstacle (a task requiring dogs to work around pole obstacles secured in a straight line) when the owner was located in their left visual hemifield compared to when they were in the right one [3]. Given that in a dog's brain the right hemisphere neural structures are mainly fed by inputs from the left visual hemifield and vice versa (crossed fibers at the optic nerve level are more than 70% [5]), these results support the general hypothesis of right hemisphere specialization for the analysis of stimuli with high emotional valence (i.e., the owner) [6–11]. In other words, visual analysis of the owner exerted predominantly by neural pathways of the left eye (activity of the right hemisphere) was likely to increase the dogs' arousal state, distracting them during the performance of agility obstacles (resulting in longer latencies to complete the task).

A recent study has found a significant relationship between the lateralized processing of visuospatial attention and motor functions in canine species [4]. Briefly, dogs preferentially using their left paw in a motor task that required subjects to hold a puzzle feeder (namely, the "Kong test") showed a leftward bias in the total number of food items eaten from a Plexiglas board (i.e., a food detection task resembling the so-called cancellation test). Similarly, a reversed rightward bias was observed in subjects significantly preferring their right paw in the motor task; whereas, no bias was found for ambi-pawed dogs. In addition, considering the order of eating food items, the above-mentioned significant sidedness effect (left vs. right hemispace attention) was revealed only in the left-pawed group that showed a clear leftward bias (right hemisphere activity), supporting the general hypothesis of the right hemispheric superiority in spatial attention control. Apart from contributing to basic knowledge about the biology of dogs, these results could improve human abilities in canine training during different activities (animal-assisted therapy, guide dogs for the vision impaired, or sport competitions). For instance, it could be useful for a dog trainer to know the dog's visuospatial orienting bias in order to choose the best strategy to interact with it during training (e.g., to optimize the capture of his attention and/or to choose the handling side that interferes less with his orienting attention).

In light of the previous research evidence, the present study aimed at investigating the influence of laterality on sheepdog training and on their selection, evaluating the dogs' turning motor pattern around the herd and their behavior during the first encounter with sheep in a training session.

2. Materials and Methods

2.1. Subjects

Access to 15 healthy adult dogs (*Canis familiaris*: 6 males and 9 females) was obtained through an agility dog center "Mix and Breed" in Bussero, Italy. Their ages ranged from 2 to 8 years (4.6 ± 0.45; mean years ± SEM). The studied population was composed of both pure and crossbred dogs of small, medium, and large body size. Only two males and four females were neutered. None of the observed dogs had previously been trained in sheepdog activities (see Table 1 for details). In addition, the dogs were checked by a veterinarian for the presence of estrous or mouthedness (e.g., broken canines or teeth issues), which may have biased their performance under the test conditions.

Table 1. Subjects' characteristics and their behavioral score (BS) during clockwise and counterclockwise turns. The BS was computed for each subject allocating a score of 1 for each of the behaviors analyzed.

Dog	Sex	Neutered	Age (years)	Weight (Kg)	Breed	BS Clockwise	BS Counterclockwise
Ambra	female	no	6	19	Border Collie	0	6
Chobil	male	no	4	21	Border Collie	5	7
Euforia	female	no	3	23	Belgian Tervuren	14	26
Goku	male	no	4	21	Border Collie	15	4
Gulliver	male	no	4	27	Belgian Malinois	6	25
Mimi	female	no	6	24	Belgian Groenendael	11	16
Nabi	female	yes	4	22	Belgian Malinois	0	7
Smog	male	no	3	17	Mongrel	7	7
Tuli	female	no	2	22	Belgian Groenendael	3	8
Zoe	female	no	3	16	Border Collie	2	7
Geppi	female	yes	6	17	Smooth Collie	10	13
Juno	male	yes	6	16	Australian Kelpie	5	11
Ruster	male	yes	3	17	Border Collie	5	6
Vicki	female	yes	7	10	Mongrel	7	7
Vicky	female	yes	8	20	Australian Shepherd	4	6

2.2. Procedure

Each subject was led by the owner within a large enclosed area where a group of 3 sheep was placed in the center (Figure 1). As soon as the owners reached a designated position, at a distance of about 4 meters from the sheep, they unleashed the dog and left the area. The dog's interactions with the herd were recorded using two video cameras in order to have a full view of the working area. An expert sheepdog trainer was positioned close to the sheep to promptly interrupt the dog's aggression toward the sheep by using voice commands or by shaking a black plastic envelope. The recordings lasted 6 minutes, from the dog's release till the end of the working session. The dogs were initially allowed to interact freely with the sheep, turning around the herd according to their natural movement. Subsequently, they were induced by the trainer to interrupt their spontaneous rotational movement around the sheep every 20 s (if the dog kept its own rotation around the sheep for more than 20 s, the trainer stopped the movement by placing himself between the dog and the sheep). The dogs could then resume their rotation movement in the same or the reverse direction around the sheep (see Figure 1).

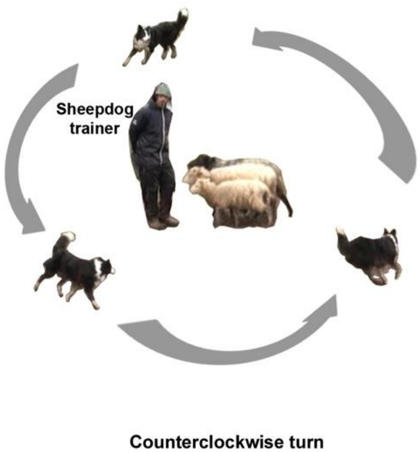

Figure 1. Schematic representation of the positions of the dog, the trainer, and the sheep during the session and an example of a dog making a counterclockwise turn around the herd.

During the dogs' spontaneous rotation movements around the herd, the trainer remained motionless to prevent any influence on the subjects' behavior, but he intervened just to interrupt the dogs' rotation movements (each 20 s) or to prevent aggression. The sheep were always the same during the tests, and they were familiar with sheepdog activities. The tests took place on three different days, during which 5 dogs were tested per day. The daily interactions of the dogs with the sheep were performed with 30 min intervals in order to give the sheep time to rest and recuperate.

2.3. Video Analysis

The recorded videos were scanned frame by frame by two trained experimenters. The following parameters, which included specific prey-driven behaviors, were analyzed [2]:

Turning preference: The total time (in s) spent turning clockwise and counterclockwise with respect to the sheep during the working session; and dogs' behavior: Straight approach—the dog approached the sheep along a straight trajectory, shoving—the dog pushed one sheep using its shoulder, gripping—the dog approached the sheep aggressively gripping and pulling its leg wool, approach direction—indicates the dog's approach direction toward the sheep (lateral, frontal, or backside approach), and sidedness—indicates the dogs' side (left or right) on which the sheep was positioned in the lateral approach.

The frequency of straight approaches, shoving, and gripping during the working session was computed for each dog, and the direction and sidedness of each approach was described. Therefore, the total frequency of the above-mentioned behaviors, as well as the total frequency of the different direction of the dog's approach toward the sheep (lateral, frontal, backside) were then obtained and analyzed.

2.4. Statistical Analysis

Data distribution was tested using the Shapiro–Wilk test; subsequently, the paired-samples *t*-test and the Wilcoxon signed-rank test were used to test parametric and nonparametric data, respectively. For all statistical tests, SPSS software was used, and the results were considered significant if $p < 0.05$.

2.5. Ethics Statement

The experiments were conducted in accordance with directive 2010/63/EU of the European Parliament and of the Council and were approved by the Department of Veterinary Medicine's (University of Bari) Ethics Committee, EC (Approval Number: 12/17); in addition, before the experiment began, informed consent was obtained from all the participants included in the study.

3. Results

3.1. Dogs' Turning Preference and Behavior

The relationship between lateralized turning motor pattern and sheepdog behavior is shown in Figure 2. Results revealed that gripping behavior occurred with a higher frequency during counterclockwise turns around the sheep compared to during the clockwise turns (clockwise turns: 1.06 ± 1.79; counterclockwise turns: 2.00 ± 3.07; $z = 80.00$, $p = 0.016$). In addition, when dogs ran in a circle around the flock in a counterclockwise direction, their approach to the sheep occurred significantly more along a straight trajectory (clockwise turns: 3.73 ± 0.53; counterclockwise turns: 5.33 ± 2.05; $t(14) = -2.323$, $p = 0.036$). Regarding shoving behavior, it is important to note that it occurred only on four occasions, and, in particular, three times during clockwise turns and only once during counterclockwise turns. No significant statistical differences were found in the total time spent by dogs turning clockwise and counterclockwise around the herd during sessions (clockwise: 53.54 ± 7.64 s; counterclockwise: 56.55 ± 8.47 s; $t(14) = -0.340$, $p = 0.739$). Dogs approached the sheep more frequently from their backside (87.5%) compared to their lateral (7.8%), and frontal (4.7%) sides. Regarding backside approaches, statistical analysis revealed that they occurred significantly more during counterclockwise than during clockwise turns (1.00 ± 0.37 and 2.73 ± 0.67, respectively; $z = 87.00$, $p = 0.003$). Although a slight tendency to approach sheep placed on dogs' left side was found it did not reach a statistical significance (right vs. left: Clockwise turns: $z = 18.00$, $p = 1.00$; counterclockwise turns: $z = 13.00$, $p = 0.579$; straight approaches: $z = 36.00$, $p = 0.383$; gripping behavior: $t(14) = 0.904$, $p = 0.381$).

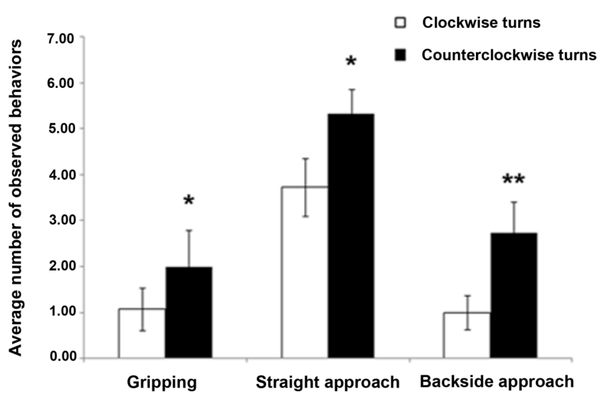

Figure 2. Dogs' behavior during clockwise and counterclockwise turns (means with SEM are shown; * $p < 0.05$; ** $p < 0.01$).

3.2. Sex Ratio

The statistical analysis revealed that female dogs approached the sheep significantly more along a straight trajectory (clockwise turns: 3.22 ± 0.98; counterclockwise turns: 5.77 ± 0.52; $t(8) = -3.603$, $p = 0.007$) and from their backside (backside approach: clockwise turns: 1.11 ± 0.53; counterclockwise turns: 2.88 ± 0.97; $z = 280.00$, $p = 0.017$) during the counterclockwise turns than during clockwise turns. No differences were found for male dogs (straight approach: $t(5) = -0.139$, $p = 0.895$; backside approach: $z = 18.00$, $p = 0.096$).

No other statistically significant differences between clockwise turns and counterclockwise turns were found in male and female dogs for the other analyzed parameters: gripping (male: $z = 7.00$, $p = 0.461$; female: $z = 16.00$, $p = 0.236$) and turning preference (male: $t(5) = -0.671$, $p = 0.532$; female: $t(8) = 0.414$, $p = 0.690$).

3.3. Age

The statistical analysis showed more backside approaches by adult dogs compared to younger ones (backside approach (2–3 years: $z = 10.00$, $p = 0.059$; 4–8 years: $z = 42.50$, $p = 0.016$)). The analysis showed no other significant differences between clockwise and counterclockwise turns in the analyzed parameters according to the dogs' age: Gripping (2–3 years: $z = 4.50$, $p = 0.414$; 4–8 years: $z = 19.50$, $p = 0.344$) and straight approach (2–3 years: $z = 9.00$, $p = 0.144$; 4–8 years: $z = 28.00$, $p = 0.160$).

4. Discussion

The most relevant finding of this research was that the expression of the dogs' aggressive behavior toward the sheep is lateralized. Specifically, among the aggressive behaviors scored, the gripping and the straight approach toward the sheep occurred with a higher frequency when the dogs ran in a circle around the livestock in a counterclockwise direction. During dogs' rotational movements the sheep were viewed mainly in their monocular peripheral vision. Considering that the lateral field of each of the dogs' eyes projects mainly to the contralateral side of the brain (crossing of fibers at the optic nerve level is 70% [5]), the visual analysis of the herd by the left visual hemifield during counterclockwise turnings indicates a prevalent activation of the right hemisphere. This result fits with previous evidences about the specialization of right neural structures of dogs' brains in attending to arousal stimuli [6–13]. Previous studies employing the head-turning paradigm reported a right hemisphere main involvement in processing visually arousing stimuli, in particular the black silhouette of a cat displaying an agonistic posture (with an arched laterally displayed body and erected tail) and a snake silhouette, which is generally considered as an alarming stimulus for most mammals [7]. Moreover, a right hemisphere dominant activity was found in the dogs' response to arousing acoustic, olfactory, and visual stimuli [8–11]. Specifically, the dogs consistently turned their head with the left ear leading (right hemisphere activation) in response to thunderstorm playbacks and conspecific and human vocalizations eliciting intense emotions [10,14]. On the other hand, the dogs consistently used the right nostril (right hemisphere) to sniff cotton swabs impregnated with arousing odors (e.g., conspecific odors collected during a stressful situation, adrenaline, and veterinarian sweat) [8,9]. In addition, a right hemisphere main involvement was found in the processing of human faces expressing intense and arousing emotions (e.g., anger and fear) [11].

Recent studies on several vertebrates have reported a general specialization of the right hemisphere in the expression of intense emotions, including aggression, escape behavior, and fear [15]. In particular, our findings are consistent with the right hemisphere specialization for aggressive responses previously reported for several species, including chicks [16], horses [17], and toads [18], which showed more aggressive responses to other conspecifics when they were positioned on the animal's left side than when they were on its right.

A reasonable explanation for the reported asymmetry in dogs' aggressive behavior toward the sheep is to assume that it reflects a different activation of the two brain hemispheres during visual analysis of the target (i.e., the sheep). In addition, neurobiological studies on rats reported that the preferred direction of rotation was contralateral to the brain hemisphere with higher levels of dopamine [19], a neurotransmitter directly involved in motor control and emotional functioning.

Prey drive is a carnivore's inborn behavioral pattern to pursue and capture prey, and it is a fundamental characteristic of sheepdogs. As a matter of fact, herding behavior is modified and influenced by predatory behavior [20]. Through selective breeding, humans have been able to reduce sheepdogs' prey-driven behavior while maintaining their hunting skills. There is now evidence that the left hemisphere neural structures are better suited for the control of prey-driven behavior in dogs [21]. A similar specialization of the left hemisphere in predatory behaviors has been documented in other species, like toads [22], zebrafish [23], and black-winged stilts [24]. An interesting explanation of the prey-driven behavior control in sheepdogs during herding could be found in the inhibition exerted by the left hemisphere on aggressive behaviors, whose expression is elicited by the right hemisphere [25]. Our results support this hypothesis, since aggressive behavior occurred predominantly during the dogs' counterclockwise rotations around the sheep (right hemisphere dominant activity). Thus, it could be hypothesized that during clockwise turning, dogs controlled the herd with the prevalent use of the left hemisphere (specialized for predatory behavior), which plays a main role in sustaining the subject's attention and in risk taking, by inhibiting a fast and emotive response mediated by the right hemisphere activation [25]. This hypothesis is supported by dogs' tendency (but not statistically significant) to express "controlled" prey-driven behaviors toward the sheep during clockwise turns (left hemisphere activation). The left hemisphere activity and its functions are fundamental for the successful pursuit and capture of prey [25]. The sheep's presence led the dogs' arousal to increase, causing a right hemisphere activation, which regulates the expression of aggressive behaviors (shown in counterclockwise turns). In particular, the dogs' perception of arousing stimuli (the sheep) and the intense emotions that the sheep's presence elicited in the tested animals resulted in the dogs' aggressive response toward the herd.

On the other hand, it could be possible that the dogs' right hemisphere activation was elicited by the trainer's presence that prevented dogs from attacking the sheep. In other words, the trainer's presence could have increased the dogs' arousal levels producing a conflicting inner state caused by the dogs' ambivalent attitude to approaching the sheep (left hemisphere) and to withdrawing from them (right hemisphere) because of the trainer's presence. As a result of this conflicting situation, the dogs' stress levels (arousal) increased and the right hemisphere took control of dogs' flight or fight behavioral response.

Apart from improving the training techniques of sheepdogs, our results contribute to defining novel parameters for the assessment of animals' emotions, which could have a potential impact on their welfare. In particular, given the right–left hemisphere specializations, the evaluation of lateralized behavioral responses to an environmental stimulus, which reflects the activation of one hemisphere, could provide information about an animal's emotional state. Dominance by the right hemisphere suggests that the animal perceives the stimulus or the situation as arousing (or stressing) and potentially leads to the expression of intense emotional expressions, including aggression [16,17]. Therefore, the assessment of lateralized patterns could help to determine whether an animal experiences a certain situation or event as positive or negative and, at the same time, it could be useful to improve and ensure human safety during interactions with the dogs.

Overall our results revealed the existence of a relationship between motor lateralization and aggressive behavior in dogs during sheepdog training, supporting previous evidences about the influence of brain lateralization on visually guided motor responses in dogs. These results have direct implications for both the personnel involved in the selection of dogs to be trained for herding and for the development of new training techniques.

Author Contributions: Conceptualization, M.S., D.B., S.d., and A.Q.; methodology, M.S., D.B., S.d., and A.Q.; formal analysis, M.S., S.d., and A.Q.; investigation, M.S., D.B., S.d., and A.Q.; data curation, M.S., D.B., S.d., and A.Q.; writing—original draft preparation, M.S., S.d., and A.Q.

Funding: This research is part of the following project: "Lateralizzazione e disturbi del comportamento nel cane" supported by the University of Bari, Italy, through a financial grant to M.S.

Acknowledgments: We are grateful to Fabrizio Pertosa for technical assistance during the experiment.

Conflicts of Interest: The authors declare no conflict of interest.

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