

Sheep laterality

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Turning preferences among 309 white-faced ewes were individually evaluated in an enclosed, artificially lit T-maze, followed by each ewe choosing either a right or left return alley to return to peers. Data recorded included time in the start box, time in the T-maze, exit arm chosen to leave the T-maze, and return alley. Right and left arms of the T-maze were chosen 65.7% and 34.3% of the time, respectively, while right and left return alleys were chosen 32.4% and 67.6%, respectively. Exit arm and return alley were not independently chosen ($p < .0001$), with observed counts being higher than expected under independence when ewes made the same choice for exit and alley (RR or LL turn patterns) and being lower than expected for alternating choices (RL or LR). Out of the 309 ewes, 28.2% and 30.1% chose RR and LL turn patterns, respectively, while 37.5% chose the RL turn pattern, but only 13 (4.2%) chose the LR turning pattern. Overall, ewes that initially turned right when presented a second turning opportunity had a slight preference to alternate their turning direction, while ewes that initially turned left tended to continue turning left when given another chance to turn. Exit arm and return alley laterality was not related ($\alpha = .05$) to time of day the test was administered, ewe's age or genetics, most recent liveweight, or most recent shorn fleece weight. The mean time spent in the start box (21 s) was not related to exit arm ($p = .947$) or return alley ($p = .779$). Mean time (15 s) spent in the T-maze was not related to exit arm ($p = .086$) or return alley ($p = .952$). More research will be required to understand sheep turning laterality and how it can impact working facilities and research equipment.

Keywords: Behavioural lateralisation; Handedness; T-maze; Livestock behaviour.

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During the 1970s biologists began to consider that behavioural lateralisation or asymmetry was possibly not just a human characteristic (Jackson, 1905) but was ubiquitous throughout the animal kingdom (Babcock, 1993). For a more in-depth understanding of vertebrate lateralisation the reader is directed to several excellent recent comprehensive reviews (Rogers, 1989; Rogers & Andrew 2002; Vallortigara & Rogers, 2005).

Stress appears to play a role in the expression of lateral tendencies. If reindeer (*Rangifer tarandus*), are driven or crowded they invariably rotate counterclockwise (leftwards); however, free-ranging reindeer apparently demonstrate no right- or left-turning preference (Espmark & Kinderås, 2002). The left-turning bias when reindeer are stressed (Rogers, 2010) suggests that it is the right hemisphere of the brain that responds to escape and other emergency responses among these animals. Recent research by Versace, Morgante, Pulina, and Vallortigara (2007) suggests that individual- and population-level lateralisation can be observed in different tasks, and behavioural lateralisation may provide insight into understanding stress responses (Morgante et al., 2007). Horses appear to be more reactive to a frightening stimulus when it is presented on the left (Austin & Rogers, 2007), suggesting that the left eye may be preferred by horses (Farmer, Krueger, & Byrne, 2010) for assessment and evaluation of unfamiliar objects. Robins and Phillips (2010) have also shown that cows demonstrate a similar left eye bias when viewing novel stimuli.

The majority of laterality studies involving ruminant livestock have been conducted using dairy cattle (Albright, 1981; Albright, Yungblut, & Arave, 1978; Albright, Yungblut, Arave, & Wilson, 1975; Arave, Lamb, Arambel, Purcell, & Walters, 1992; Arave & Walters, 1977, 1980; Beauchamp, Chapman, & Grebing, 1967; Forsberg, Pettersson, Ljungberg, & Svennersten-Sjaunja, 2008; Hopster, van der Werf, & Blokhuis, 1998; Jackson, 1905; Phillips, Llewellyn, & Claudia, 2003; Tucker, Cox, Weary, & Špinka, 2009; Uhrbrock, 1969; Yungblut, Albright, Hill, & Moeller, 1974) especially with respect to lying. Bao and Giller (1991) reported that cows with twins showed a small ($p < .01$) preference for lying on their left side both pre and post calving. Wagon and Rollins (1972) found that cows appear to lie predominantly on their left sides especially in the afternoon following a mid-morning feeding. Although dairy cattle show consistency in side of the milking parlour they prefer (Mateus, daCosta, & Broom, 2001), apparently no statistically significant level of discomfort or stress was recorded if they were milked on the non-preferred side of the parlour. These results suggest that the phenotypic expression of laterality is complex and probably cannot be attributable to only simple causes.

In contrast to cattle, many fewer studies exist on lateralisation in sheep (Lane & Phillips, 2004). Using 10 Suffolk ewes, Hansen et al. (1978) reported that individual ewes varied ($p < .001$) in their preference to use either the

right or left arm when exiting a T-chute based on four trials. Overall, the left arm of the T-chute was chosen 62.5% of the time. However, two ewes turned right 100% of the time, five ewes turned left $\geq 75\%$ of the time (of which four ewes turned left 100% of the time) while three sheep showed no laterality preference for turning (50% right and 50% left). These authors concluded individual animals had a tendency to turn in one direction, but with only four trials right or left preferences should not be assigned. Recently Erhard, Boissy, Rae, and Rhind, (2004) demonstrated that female sheep, if on a limited nutrition regime during early gestation, produced female offspring that had a left bias ($p < .05$) in a T-maze. Lane and Phillips (2004) found that neither gender nor number of siblings influenced laterality among 54 neonatal lambs. Simitzis et al. (2009) found that male lambs between 2 and 5 months of age had a tendency of turning to the right-hand side of their test pen irrespective of nutritional treatments.

MAZES

The single T-maze probably represents the simplest maze in use today (Silverman, 1978) yet it is not free of introducing bias. Mazes can be considered complex environments (Liddell, 1925b; Silverman, 1978) requiring the animal to demonstrate neural processes controlled by multiple sensory stimuli, both internal and external to the maze itself. Walker, Dember, Earl, and Karoly (1955) indicated that when an animal was returned to a maze, it would likely use the same exit the second time, especially if it had been positively rewarded initially (Barnett, 1958). Furthermore, the route by which rats are taken to the test apparatus may have an effect on their subsequent behaviour in the maze (Munn, 1933). Grandin, Odde, Schutz, and Behrns (1994) found that this response held for cattle, since cattle resisted change by looking back and forth at the decision point in a Y-maze once they associated a specific treatment effect with a specific side of a maze and the treatment was then switched.

Lambs exhibit a strong spatial memory (Nowak, 1994) and can learn simple tasks in as few as two trials (Bremner, Braggins, & Kilgour, 1980). Adult sheep have been shown to "learn" in a single trial, especially if the experience to which they are subjected is unpleasant (Hutson & Butler, 1978). Sheep exhibit good memory, as they can remember where "home" is and will remain in specific locations on the landscape without fencing through a process called hefting (Hart, 2004). Under experimental conditions sheep have been shown to remember experimental protocols for up to 6 weeks (Morton & Avanzo, 2011). Therefore, each of the sheep evaluated in this study were exposed only once to the T-maze to eliminate a learning bias. Knowing how each of the sheep used in this study had been handled from birth until they were evaluated in the T-maze was not considered essential

because Hosoi, Rittenhouse, Swift, and Richards (1995) suggest that ungulates may find a maze environment completely atypical, and as such the data may reflect behaviours quite unrelated to what may occur in its natural environment and daily habitat. Furthermore, Price and Thos (1980) suggest that effects of rearing are minimal during short-term social isolation of sheep. In this study the protocol applied to each age class of sheep was consistent among years and followed routine extensive husbandry practices (Mathis & Ross, 2000). Furthermore, the ewes evaluated in this study were tested only once and had never previously been tested in a T-maze. Therefore, the objective of this research was to evaluate white-faced ewe laterality when exiting an enclosed T-maze followed by their choosing one of two return alley routes to return to peers.

METHOD

The T-maze

The data used in this study were collected prior to the USDA-ARS Jornada Experimental Range livestock research programme participating under the guidelines of the New Mexico State Universities Institutional Animal Care and Use Committee's protocol. However the senior author, who is currently on this committee at NMSU, can attest to the fact that this study was conducted with the highest regard for the animal's health and welfare and that none of the 309 ewes was mishandled or harmed in any way prior to, during, or following the study.

The T-maze (Figure 1A) was constructed in a location remote from human traffic and other animals in an attempt to reduce external cues that could have influenced the sheep's behaviour once it was put inside the T-maze. In addition the pens constructed to hold pre- and post-tested sheep were located behind the door opening into the start box. Pen D held the sheep immediately before they were tested. Its solid sides prevented sheep returning from the T-maze from being seen by those sheep yet to be tested. Similar precautions have been used with cattle (Robins & Phillips, 2010) to reduce the confounding effects that familiarisation with both the testing procedure and the novelty of the protocol may have on animals yet to be evaluated. The wooden T-maze consisted of two sides and a roof constructed of unpainted commercially available plywood sheets and pine lumber. It did not have a floor but sat directly on the soil. The joints between adjacent plywood sheets were sealed to prevent sunlight from entering the maze. To exclude sunlight from entering through the start-box doorframe, a foam seal was maintained around the opening to exclude light once it was closed (Figure 1B). A viewing port located above and to the right of the entrance door into the start box (Figure 1B) gave an observer, standing outside the

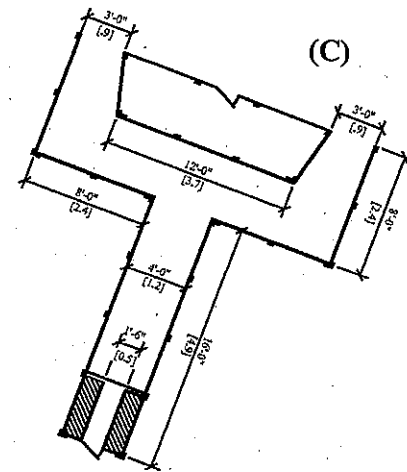
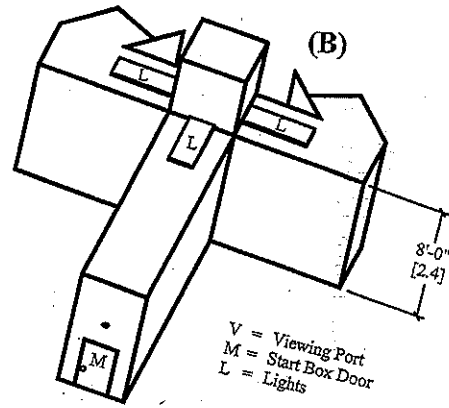
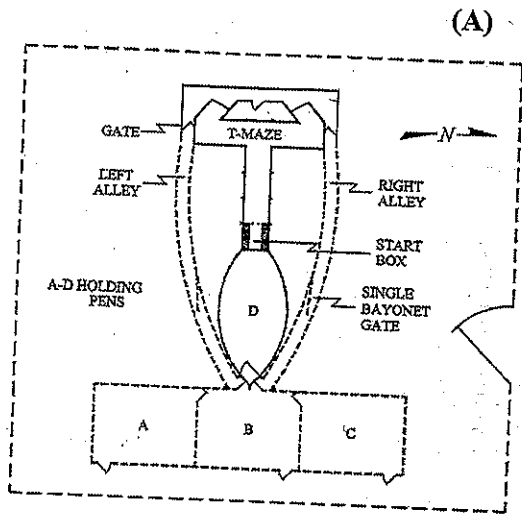


Figure 1. Three views of an enclosed plywood T-maze that sits directly on the soil, for evaluating sheep laterality behaviour. Corral and associated T-maze structures constructed of solid wood {-} and wire {- -} not to scale (A); 3-D representation of the T-maze with height dimensions in feet and [metres] (B); and a plan view of the T-maze with length dimensions in feet and [metres] (C).

T-maze, the ability to watch the sheep while it was inside the T-maze. The viewing port was also surrounded by foam rubber to exclude external light from entering the T-maze. The inside of the T-maze was illuminated by twelve 40-watt fluorescent tube-lights located in three ceiling fixtures positioned at the intersection of the arms of the T-maze (Figure 1B). This placement kept the start box dimly illuminated compared to the intersection. Grandin (1990) found that sheep prefer to move from a dimly illuminated area to a more brightly illuminated area. Electricity was provided by a portable gasoline generator located approximately 24 m north and east of Pen D.

The longest runway in the T-maze (Figure 1C) was 4.9 m (16.1'). The left and right exit arms or branches as they have been called (Heird, Lennon, & Bell, 1981) were each 2.4 m (7.8') long and extended at 90° angles on either side of the 3.7 m (12.1') long runway. The 1.2 m (3.9') × 0.5 m (1.5') start box was located in the centre of the 1.2 m (3.9') wide runway just inside the door through which animals entered the T-maze.

The T-maze was oriented so sheep entered through the south end and exited through either a left (south) or right (north) arm (Figure 1B). To ensure the right and left exit arms provided similar sensory stimulation among sheep, especially illumination and wind movement, the exit arms were narrowed to 0.9 m (3.0') and were covered with plywood (Figure 1B and 1C). Franklin and Hutson (1982) demonstrated that sheep used both arms of a Y-maze equally when one had been traversed 25 times by a group of 20 sheep leaving visual cues including footprints, wool, and faeces while the other arm was "clean". This is in contrast to Liddell (1925a) who reported that even a few small tufts of grass and seeds in his labyrinth tended to interrupt the movement of sheep through his test apparatus. Therefore the day before each test all plant material in or on the soil was pulled and raked out of the T-maze and the soil inside the maze was wetted to eliminate dust during testing. Immediately preceding testing the soil floor inside the T-maze was again raked to eliminate all foreign objects including animal tracks. Raking was repeated after every twentieth animal tested. This was less frequent than the schedule by Kilgour (1981) who raked his test apparatus following the testing of every third cow to obliterate animal tracks. However, if it was necessary for a technician to enter the T-maze for any reason prior to the twentieth animal being tested, the T-maze was raked to eliminate both human and animal tracks.

Weather parameters recorded included ambient wet and dry air temperatures outside and inside the T-maze, along with outside atmospheric conditions throughout the 2-day study. Temperatures inside the maze were recorded at the intersection of the long alley and exit arms.

Animals and testing procedure

A total of 309 white-faced range ewes between 8 months and 10 years of age were each evaluated in a single trial for turning laterality when exiting the enclosed T-maze on 30 and 31 January 1997. The genetics of these sheep represented straight Polypay and $3/4$ Polypay \times $1/4$ Rambouillet breeding. The night before testing the sheep had been provided with *ad libitum* drinking water and a restricted amount of feed. Just prior to testing ewes were moved to Pens A through C (Figure 1A). Once the ewes were moved into Pen D they were sequentially (non-randomly) selected based on which was closest to the door leading into the start box. Two technicians then gently moved the sheep through the plywood door of the T-maze and into the start box. A stopwatch was immediately activated as the entrance door was shut behind the sheep and one of the technicians standing in Pen D behind the closed plywood door began watching the animal through the viewing port with his right eye. An open-mesh counterbalanced guillotine gate at the front of the start box was left in the closed position for a minimum of 10 s to allow the animal time to orient itself to its surroundings. Only after 10 s—or longer if necessary to ensure that the animal's head was observed to be oriented towards the exit arms—was the guillotine gate raised by pulling on a rope activated by the technician watching the animal through the viewing port. The open position of the guillotine gate was maintained until the ewe was no longer visible in the T-maze. At that time the guillotine gate was allowed to drop shut with a bang. The sound generated by this procedure might have hastened the ewe's return to peers through the return alley; however, its exact effect on the ewes was not evaluated.

If the animal did not immediately leave the start box, at the end of 60 s the plywood door leading into the start box was opened and the animal was given a gentle prod. When a prod had to be administered, the animal's ID along with notes on the animal's reaction to the prod was recorded. Once the animal stepped into the long runway of the T-maze the first stopwatch was stopped and a second stopwatch was activated. The second stopwatch was stopped when no fleece on the ewe was observed through the viewing port as the animal moved out of the T-maze through either the right or left exit arms. At the point where the ewe was no longer visible through the viewing port the second stopwatch was stopped and the guillotine gate was released. The second stopwatch recorded the time the animal spent in the T-maze, which has been referred to by Kratzer, Netherland, Pulse, and Baker (1977) as the animal's "latency of escape". In addition to time in the start box and latency time, the right or left T-maze exit arm chosen and the right or left return alley chosen to return to Pen B (Figure 1A) were recorded for each animal.

Statistics

Percents, standard errors, and approximate 95% confidence intervals (*CI*) (Snedecor & Cochran, 1967, p. 210) were calculated for the categorical responses: maze exit (right or left), return alley (right or left), and the four combinations of maze exit and return alley. Mean responses between right versus left choice (for maze exit and alley return) were compared using two-sample *t*-tests (with homogeneity of variance being checked by *F*-test) for the numeric responses: time in start box, time in maze, fleece weight, sheep liveweight, and individual sheep's percent Polypay. Chi-square tests of homogeneity were performed for right/left maze exit and right/left return alley versus age of sheep (in years) and hour tested. Lastly a chi-square test of independence was performed for right/left maze exit versus right/left return alley. All analyses were performed using SAS procedures (SAS Institute, 1989, 1990).

RESULTS

Wet and dry bulb ambient air temperatures ranged between $<-1^{\circ}\text{C}$ ($< 30^{\circ}\text{F}$) at 0710 hr to a 20°C (68°F) at 1415 hr over the 2-day study (January 3–31, 1997). Overall, temperatures inside the maze were about 0.5°C (1°F) warmer than outside the maze throughout the study. Both days were clear with no wind to intermittent wind out of the west north-west and south south-west. Furthermore, the ambient weather conditions (as indicated by hour tested) did not appear to influence exit arm ($p = .179$) or return alley ($p = .818$) chosen.

A summary of percents (with 95% confidence intervals) for choice of right/left T-maze exit and right/left return alley for the 309 ewes in this study is given in Table 1. Neither direction of turning when exiting the T-maze nor the alley chosen to return to peers occurred with equal probability (50/50) among the 309 ewes. Right and left arm of the T-maze were chosen 65.7% and 34.3% of the time, respectively. In contrast the right and left return alleys were chosen 32.4% and 67.6%, respectively. T-maze exit arm and return alley were not independently chosen ($p < .0001$), with observed counts being higher than expected under independence when ewes made the same choice for exit and alley (RR or LL turn patterns) and being lower than expected for alternating choices (RL or LR). Specifically, out of the 309 ewes, 28.2% and 30.1% chose RR and LL turn patterns, respectively, while 37.5% chose the RL turn pattern, but only 13 out of 309 (4.2%) ewes chose the LR turning pattern. A slightly different interpretation of these data is to consider the choice of return alley conditioned on the initial exit choice. Thus, of the 203 ewes choosing the right arm, 116 (57.1%) demonstrated an alternating RL turning preference in choosing the left alley, while 87 (42.9%) of those ewes

TABLE 1
Results

Arm	Alley		Row statistics
	Left	Right	
<i>Left</i>			
Observed frequency	93	13	106
Expected frequency ^b	71.7	34.3	
Percent out of 309	30.1	4.2	34.3
Confidence interval ^{c,d}	(L = 25.0, U = 35.2)	(L = 2.0, U = 6.4)	(L = 29.0, U = 39.6)
<i>Right</i>			
Observed frequency	116	87	203
Expected frequency ^b	137.3	65.7	
Percent out of 309	37.5	28.2	65.7
Confidence interval ^{c,d}	(L = 32.1, U = 42.9)	(L = 23.2, U = 33.2)	(L = 60.4, U = 71.0)
<i>Column statistics</i>			
Observed frequency	209	100	
Percent out of 309	67.6	32.4	
Confidence interval ^{c,d}	(L = 62.4, U = 72.8)	(L = 27.2, U = 37.6)	

Chi-square test^a with 95% confidence intervals for independence among 309 ewes each tested once when exiting an enclosed T-maze and their returning to peers located behind the T-maze through one of two open return alleys.

^aOverall $\chi^2 = 29.78$, $p < .0001$ with 1df.

^bExpected frequency under independence between T-maze choice and return alley choice.

^cL = Lower confidence limit.

^dU = Upper confidence limit.

returned to peers through the right alley (RR). Of the 106 ewes exiting through the left arm, 93 (87.7%) demonstrated a non-alternating (LL) turning laterality by returning to peers through the left alley. In contrast, only 12.3% of those 106 ewes demonstrated an alternating (LR) laterality. Those ewes that exited the T-maze through the left arm but returned to peers through the right alley had a statistically smaller confidence interval compared to the confidence intervals for the other three turning combinations. This test facility did not present the ewes with identical conditions at the two locations (arm and alley) where turning decisions had to be made. Our intra-maze and extra-maze environments were definitely different. Light, shadow, and wind cues were kept constant or eliminated in our intra-maze environment while our extra-maze environment was highly influenced by biotic as well as abiotic cues.

Overall, the ewes spent between 11 s and 185 s in the start box and between 4 s and 136 s for latency times. Mean time (21 s) in the start box was not related to exit arm ($p = .947$) or return alley ($p = .779$) chosen. On only three occasions was it necessary to prod the ewes to get them to leave the

start box. Mean latency time (15 s) may have had some effect on exit arm chosen ($p = .086$) while return alley and mean latency time appeared unrelated ($p = .952$). Age of our ewes (between 8 months and 10 years) was not related to exit arm ($p = .356$) or return ally ($p = .504$) chosen. Furthermore, neither amount of wool that had been shorn in 1996, the individual's most recent liveweight taken in 1996, or the sheep's genetic make-up appeared to have had any significant relationship on arm chosen by any of the sheep when exiting the T-maze ($p = .314, .649, \text{ and } .905$, respectively) or the return alley they used to return to peers once they were outside the T-maze ($p = .748, .403, \text{ and } .154$, respectively).

Of the 309 ewes, only 3 were slow or deliberate in exiting the maze. These three sheep appeared to be observing the plywood sides and ceiling, and returned into the start box, smelling it and the soil, but did not appear to be under stress. Of the remaining sheep, 305 moved without running but with determination unidirectionally down the centre of the long runway without touching the T-maze walls and without vocalising. Although movement of the ewes through the T-maze appeared free and unconstrained, some ewes did stop or momentarily hesitate at the intersection of the exit arms as if they were deciding which way to turn. The T-maze was entered only once by technicians to remove one animal that would not exit on its own. Based on a priori protocol the soil was raked after this event. However, once outside the T-maze a few sheep, not individually identified, hesitated or turned around at various points before passing through the single bayonet gates (Anderson & Smith, 1980) located in each of the two return alleys that returned the sheep to their peers.

DISCUSSION

This research appears to be the first to report on turning laterality of ewes when leaving an enclosed T-maze to return to peers through either a right or left return alley using a single trial thus eliminating learning or memory from entering into the interpretation of the data. Our data showed both alternating and non-alternating turning laterality among the ewes evaluated when exit arm and return alley were considered together. Although exploratory behaviour has been attributed to alternation turning lateralities among rat movements through a maze (Montgomery, 1952) this may not be a completely satisfactory explanation for interpreting our results, since our intra- and inter-maze environments were very different and subtle cues can be extremely important in affecting animal behaviour (Pfungst, 1965). One obvious cue that might have differed between the inside and outside of our T-maze was the resonant sound coming from the gasoline generator through the earth and various wood and metal structures surrounding and comprising the T-maze. There might have been environmental cues recognised by the

ewes but missed by the technicians that were important in influencing the exit alley chosen by the sheep.

The docile behaviour of our sheep during testing may reflect their prior habituation to human handling as a result of their frequent interaction with technicians since birth. Although an explanation is not given, Morton and Avanzo (2011) found they could individually test 5-month-old female Welsh Mountain sheep for periods lasting up to 30 minutes without the animals showing signs of isolation distress. Furthermore, understanding why our ewes were docile, besides not being vocal as were Liddell's (1925b) sheep that bleated almost continuously in his first trial, will require further research.

Additional observations suggest that our ewes were not fearful during the time they were inside the T-maze. The majority left the start box without hesitation. This was in contrast to Liddell's (1925b) sheep that hesitated in leaving their starting compartment. He interpreted this hesitation to be due to timidity or nervousness. However, some of our ewes hesitated momentarily at the intersection of the long arm with the exit arms as if deciding which way to turn. A similar behaviour has been reported to occur with rats (Small 1901). Furthermore, our ewes did not touch the sides of the T-maze as they moved from the start box through either exit arm. Sluckin (1972) would explain this lack of thigmotaxis as indicating lack of fear. We believe the motivating force that moved our sheep through the maze was their desire to return to peers. Peers were also successfully used by Lee, Colegate, and Fisher (2006) to move sheep through their maze without solid sides. Overall, the interpretation of data from T-maze tests involves both anatomic and environmental factors, thus making accurate explanations complicated (Warren, 1958). The challenge in a complete and accurate interpretation of these data lies in the fact that a standardised test for determining laterality in livestock does not exist and as such hinders in developing the science of applied ethology as stated by Forkman, Boissy, Meunier-Salaün, Canali, and Jones (2007).

Animal management today should foster low-stress animal handling (Smith, 1998). Therefore, pro-active husbandry that focuses on understanding an animal's behavioural lateralisation should minimise stress and promote positive animal welfare (Morgante & Vallortigara, 2009; Robins & Phillips, 2010). There is evidence to suggest that applying knowledge of laterality to husbandry practices can positively impact such things as reproductive performance in cows (Rizhova & Kokorina, 2005). Therefore, if the majority of sheep are found to have an initial bias to turn right (clockwise), it may be preferable to build sheep-working facilities that curve counterclockwise to foster low-stress animal handling. A working facility that initially causes sheep to turn clockwise might tend to cause sheep to crowd together into a tighter mob as a result of "centripetal behaviour", thus making it more challenging to move individual animals through an alley or a race. In contrast, a facility that moves sheep initially in a counterclockwise

direction might tend to produce "centrifugal behaviour" that may separate individuals from the perimeter of a group and subsequently allow them to move more rapidly through an alley or race. Obviously such conjecture will require testing to determine its practicality.

One practical application in knowing if there is a predictable relationship between laterality and leadership as well as a lateralised responses to auditory signals may be in choosing which individuals to instrument and how intense the cues need to be when using directional virtual fencing (DVF™; Anderson, 2007). This method of managing animals relies on producing directional changes in a free-ranging animal's direction of movement by applying audio as well as electrical stimulation cues to either the animal's right or left side to elicit movement in the direction opposite the side to which the cues are applied. Possibly, stimulating movement towards the side reflecting an animal's innate lateral tendency may require less-intense cues compared to those required to move animals in the opposite direction. Our findings agree with Vallortigara, Rogers, and Bisazza (1999) that vertebrate animal's exhibit functional lateralisation.

CONCLUSIONS

Among 309 white-faced ewes, 8 months to 10 years of age, naïve to a T-maze, different turning lateralities were demonstrated. Those ewes that initially turned right to exit the T-maze when presented a second turning opportunity (alley to return to peers) showed a slight preference to alternate their turning direction. In contrast, ewes that initially turned left when leaving the T-maze tended to continue turning left when given another chance to turn and returned to peers in a left return alley. An accurate explanation of these turning lateralities will require further research. Furthermore, age of the sheep ($p = .356$), time of day between 0800 and 1500 hr when testing was done ($p = .179$), seconds spent in the start box ($p = .947$), and latency within the T-maze ($p = .086$) were not shown to be statistically related to laterality. Not only may T-mazes serve as a method of presenting animals pairs of choices within a research context, but also the use of mazes may provide insight into developing more efficient and humane animal-handling procedures.

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REFERENCES

- Albright, J. L. (1981). *Behaviour and management of high yielding dairy cows*. International Stockman's School, San Antonio, Texas. Clovis, CA: Agriservices Foundation.

- Albright, J. L., Yungblut, D. H., & Arave, C. W. (1978). Laterality of dairy cows. *20th International Dairy Congress, Paris, France*, 26–30, 152–153.
- Albright, J. L., Yungblut, D. H., Arave, C. W., & Wilson, J. C. (1975). Bovine laterality: Resting behaviour. In *Proceedings of the Indiana Academy of Science*. Indianapolis, IN: Butler University.
- Anderson, D. M. (2007). Virtual fencing – past, present and future. *The Rangeland Journal*, 29(1), 1–14.
- Anderson, D. M., & Smith, J. N. (1980). A single bayonet gate for trapping range cattle. *Journal of Range Management*, 33, 316–317.
- Arave, C. W., Lamb, R. C., Arambel, M. J., Purcell, D., & Walters, J. L. (1992). Behaviour and maze learning ability of dairy calves as influenced by housing, sex and sire. *Applied Animal Behaviour Science*, 33, 149–163.
- Arave, C. W., & Walters, J. L. (1977). *Factors affecting laterality of dairy animals in late pregnancy*. American Dairy Science Association 72nd Annual Meetings, Ames, IA.
- Arave, C. W., & Walters, J. L. (1980). Factors affecting lying behaviour and stall utilization of dairy cattle. *Applied Animal Ethology*, 6, 369–376.
- Austin, N. P., & Rogers, L. J. (2007). Asymmetry of light and escape turning responses in horses. *Laterality*, 12(5), 464–474.
- Babcock, L. E. (1993). The right and the sinister. *Natural History*, 102(7), 32–39.
- Bao, J., & Giller, P. S. (1991). Observations on the changes in behavioural activities of dairy cows prior to and after parturition. *Irish Veterinary Journal*, 44, 4–6.
- Barnett, S. A. (1958). Exploratory behaviour. *General Psychology*, 49(4), 289–310.
- Beauchamp, K. L., Chapman, A., & Grebing, C. (1967). Response by the calf to stimulus change. *Psychonomic Science*, 9(3), 125–126.
- Bremner, K. J., Braggins, J. B., & Kilgour, R. (1980). Training sheep as “leaders” in abattoirs and farm sheep yards. *Proceedings of the New Zealand Society of Animal Production*, 40, 111–116.
- Erhard, H. W., Boissy, A., Rae, M. T., & Rhind, S. M. (2004). Effects of prenatal undernutrition on emotional reactivity and cognitive flexibility in adult sheep. *Behavioural Brain Research*, 151, 25–35.
- Espmark, Y., & Kinderås, K. (2002). Behavioural lateralisation in reindeer. *Rangifer*, 22, 51–59.
- Farmer, K., Krueger, K., & Byrne, R. W. (2010). Visual laterality in the domestic horse (*Equus caballus*) interacting with humans. *Animal Cognition*, 13, 229–238.
- Forkman, B., Boissy, A., Meunier-Salaün, M.-C., Canali, E., & Jones, R. B. (2007). A critical review of fear tests used on cattle, pigs, sheep, poultry and horses. *Physiology and Behaviour*, 92, 340–374.
- Forsberg, A.-M., Pettersson, G., Ljungberg, T., & Svennersten-Sjaunja, K. (2008). A brief note about cow lying behaviour – Do cows choose left and right lying side equally? *Applied Animal Behaviour Science*, 11, 32–36.
- Franklin, J. R., & Hutson, G. D. (1982). Experiments on attracting sheep to move along a laneway. I. Olfactory stimuli. *Applied Animal Ethology*, 8, 439–446.
- Grandin, T. (1990). Design of loading facilities and holding pens. *Applied Animal Behaviour Science*, 28, 187–201.
- Grandin, T., Odde, K. G., Schutz, D. N., & Behrns, L. M. (1994). The reluctance of cattle to change a learned choice may confound preference tests. *Applied Animal Behaviour Science*, 39, 21–28.
- Hansen, P. J., Esch, M. W., Hinds, F. C., Brown, D. E., Cabb, A. R., & Lewis, J. M. (1978). Footedness and lateral preference in sheep. In *Update 78, DSAC 6, A Research Report of the Dixon Springs Agriculture Center* (pp. 211–214). Urbana-Champaign, IL: University of Illinois.
- Hart, E. (2004). *Hefing in practice the ancient craft of grazing the open hills*. Ludlow, UK: Caynham House.
- Heird, J. C., Lennon, A. M., & Bell, R. W. (1981). Effects of early experience on the learning ability of yearling horses. *Journal of Animal Science*, 53, 1204–1209.

- Hopster, H., van der Werf, J. T. N., & Blokhuis, H. J. (1998). Side preference of dairy cows in the milking parlor and its effects on behaviour and heart rate during milking. *Applied Animal Behaviour Science*, 55, 213–229.
- Hosoi, E., Rittenhouse, L. R., Swift, D. M., & Richards, R. W. (1995). Foraging strategies of cattle in a Y-maze: Influence of food availability. *Applied Animal Behaviour Science*, 43, 189–196.
- Hutson, G. D., & Butler, M. L. (1978). A self-feeding sheep race that works. *Journal of Agriculture*, 76, 335–336.
- Jackson, J. (1905). *Ambidexterity*. London: Kegan Paul, Trench, Trubner & Co.
- Kilgour, R. (1981). Use of the Hebb-Williams closed-field test to study the learning ability of Jersey cows. *Animal Behaviour*, 29, 850–860.
- Kratzer, D. D., Netherland, W. M., Pulse, R. E., & Baker, J. P. (1977). Maze learning in quarter horses. *Journal of Animal Science*, 46, 896–902.
- Lane, A., & Phillips, C. (2004). A note on behavioural laterality in neonatal lambs. *Applied Animal Behaviour Science*, 86, 161–167.
- Lee, C., Colegate, S., & Fisher, A. D. (2006). Development of a maze test and its application to assess spatial learning and memory in Merino sheep. *Applied Animal Behaviour Science*, 96, 43–51.
- Liddell, H. S. (1925a). The behaviour of sheep and goats in learning a simple maze. *American Journal of Psychology*, 36, 544–552.
- Liddell, H. S. (1925b). The relation between maze learning and spontaneous activity in the sheep. *Journal of Comparative Psychology*, 5, 475–483.
- Mateus, J. R., daCosta, P., & Broom, D. M. (2001). Consistency of side choice in the milking parlour by Holstein-Friesian cows and its relationship with their reactivity and milk yield. *Applied Animal Behaviour Science*, 70, 177–186.
- Mathis, C. P., & Ross, T. (2000). *Sheep production and management*. NM Cooperative Extension Service 100 B-15, College of Agriculture and Home Economics, Las Cruces, NM.
- Montgomery, K. C. (1952). Exploratory behaviour and its relation to spontaneous alternation in a series of maze experiments. *Journal of Comparative Psychology*, 45, 50–57.
- Morgante, M., Giancesella, M., Stelletta, C., Versace, E., Cannizzo, C., Ravarrotto, L., et al. (2007). Short-term adaptive response in strongly versus weakly lateralised dairy ewes. *Italian Journal of Animal Science*, 6(Suppl. 1), 567–569.
- Morgante, M., & Vallortigara, G. (2009). Animal welfare: Neuro-cognitive approaches. *Italian Journal of Animal Science*, 8(Suppl. 1), 255–264.
- Morton, A. J., & Avanzo, L. (2011). Executive decision-making in domestic sheep. *PLoS ONE*, 6(1), 15752.
- Munn, N. L. (1933). The role of sensory processes in maze behaviour, Chapter IV. In N. L. Munn (Ed.), *An introduction to animal psychology the behaviour of the rat* (pp. 155–205). New York: Houghton Mifflin Co.
- Nowak, R. (1994). Mother location by newborn lambs in repetitive testing: Influence of first successful reunion. *Applied Animal Behaviour Science*, 41, 75–86.
- Pfungst, O. (1965). *Clever Hans the horse of Mr. von Osten*. New York: Holt, Rinehart & Winston, Inc.
- Phillips, C. J. C., Llewellyn, S., & Claudia, A. (2003). Laterality in bovine behaviour in an extensive partially suckled herd and an intensive dairy herd. *Journal of Dairy Science*, 86, 3167–3173.
- Price, E. O., & Thos, J. (1980). Behavioural responses to short-term social isolation in sheep and goats. *Applied Animal Behaviour Science*, 6, 331–339.
- Rizhova, L. Y., & Kokorina, E. P. (2005). Behavioural asymmetry is involved in regulation of autonomic processes: Left side presentation of food improves reproduction and lactation in cows. *Behavioural Brain Research*, 161, 75–81.
- Robins, A., & Phillips, C. (2010). Lateralised visual processing in domestic cattle herds responding to novel and familiar stimuli. *Laterality*, 15, 514–534.

- Rogers, L. J. (1989). Laterality in animals. *International Journal of Comparative Psychology*, 3, 5–25.
- Rogers, L. J. (2010). Relevance of brain and behavioural lateralisation to animal welfare. *Applied Animal Behaviour Science*, 127, 1–11.
- Rogers, L. J., & Andrew, R. J. (2002). *Comparative vertebrate lateralisation*. New York: Cambridge University Press.
- SAS Institute Inc. (1989). *SAS/STAT® User's guide, version 6* (4th ed.). (Vol 2). Cary, NC: SAS Institute Inc.
- SAS Institute Inc. (1990). *SAS® Procedures guide, version 6* (3rd ed.). Cary, NC: SAS Institute Inc.
- Silverman, P. (1978). *Animal behaviour in the laboratory*. New York: Pica Press.
- Simitzis, P. E., Charismiadou, M. A., Kotsampasi, B., Papadomichelakis, G., Christopoulou, E. P., Papavaslopoulou, E. K., et al. (2009). Influence of maternal undernutrition on the behaviour of juvenile lambs. *Applied Animal Behaviour Science*, 116, 191–197.
- Sluckin, W. (1972). *Early learning in man and animal*. Cambridge, MA: Schenman Publishing Co.
- Small, W. S. (1901). Experimental study of the mental processes of the rat. II. *American Journal of Psychology*, 12, 206–239.
- Smith, B. (1998). *Moving 'em; a guide to low stress animal handling*. Kamuela, HI: The Graziers Hui.
- Snedecor, W. G., & Cochran, W. G. (1967). *Statistical methods* (6th ed). Ames, IA: The Iowa State University Press.
- Tucker, C. B., Cox, N. R., Weary, D. M., & Špinka, M. (2009). Laterality of lying behaviour in dairy cattle. *Applied Animal Behaviour Science*, 120, 125–131.
- Uhrbrock, R. S. (1969). Bovine laterality. *Journal of General Psychology*, 115, 77–79.
- Vallortigara, G., & Rogers, L. J. (2005). Survival with an asymmetrical brain: Advantages and disadvantages of cerebral lateralisation. *Behavioural and Brain Sciences*, 28, 575–633.
- Vallortigara, G., Rogers, L. J., & Bisazza, A. (1999). Possible evolutionary origins of cognitive brain lateralisation. *Brain Research Reviews*, 30, 164–175.
- Versace, E., Morgante, M., Pulina, G., & Vallortigara, G. (2007). Behavioural lateralisation in sheep (*Ovis aries*). *Behavioural Brain Research*, 184, 72–80.
- Wagnon, K. A., & Rollins, W. C. (1972). Bovine laterality. *Journal of Animal Science*, 35, 486–488.
- Walker, E. L., Dember, W. N., Earl, R. W., & Karoly, A. J. (1955). Choice alternation: I. Stimulus vs. Place vs. Response. *Journal of Comparative and Physiological Psychology*, 48, 19–23.
- Warren, J. M. (1958). The development of paw preferences in cats and monkeys. *Journal of General Psychology*, 93, 229–236.
- Yungblut, D. H., Albright, J. L., Hill, D. L., & Moeller, N. J. (1974). Effect of stall location and surface materials upon cow preference, stall use, cleanliness, udder health and laterality in free stall dairy barns. *Journal of Dairy Science*, 57, 630.