LATERALIZATION IN FERAL, PRZEWALSKI AND DOMESTIC HORSES

Nicole Peta Austin, BSc, Monash University Grad. Dip. Sci., University of New England

A thesis submitted for the Degree of Doctor of Philosophy of the University of New England December, 2010

ACKNOWLEDGEMENTS

I would like to thank my principal supervisor Prof. Lesley Rogers for her invaluable guidance and advice throughout my candidature. I have learned a great deal about animal behaviour from her and I am grateful for the time she has spent teaching me and sharing her extensive knowledge with me. I also thank my co-supervisor Prof. Gisela Kaplan for her equally valuable knowledge, encouragement and support. I very much appreciate the efforts of both my supervisors in making this research possible and feel I have learned from the best.

I am also very grateful to all the owners of the domestic horses that were studied. I would like to thank the Djabugay Aboriginal People, especially the Brim family, for giving me permission to stay and observe the feral horses at Mona Mona Aboriginal Mission. I thank the National Parks and Wildlife Service, who assisted me in my research by allowing me to observe the feral horses and provided transport to the study site in Oxley Wild Rivers National Park, and especially Mr Kenneth Pines. I would also like to thank Dr Claudia Feh and the Association pour le cheval de Przewalski: TAKH for allowing me to observe the Przewalski horses, and especially Dr Marthe Kiley-Worthington for making this possible and for allowing me to observe her Arab horses, giving me advice and providing accommodation at the Centre for Eco-Ethos Research and Education. I have gained much knowledge from all these people.

I would very much like to thank Patrick Wilms for his invaluable support and encouragement, and his assistance while I was conducting fieldwork in North Queensland; it is much appreciated. I am also grateful for the support, discussions and ideas shared with the students in the Centre for Neuroscience and Animal Behaviour, including Dr. Adam Koboroff, Leanne Stewart, Dianne Gordon, Caralyn Kemp, Kelly O'Shea, Megan English, Julian Brown and Penny Macintyre.

ABSTRACT

Lateralization, referring to differential processing of information by the left and right sides of the brain and to side biases in behaviour, has been reported in domestic horses. To determine whether lateralization is characteristic of the horse (Equus caballus) as a species and not simply a result of training or domestication, field studies were carried out observing Przewalski horses (Equus ferus przewalski) and two groups of feral horses that differed in number of generations removed from domestication. Przewalski horses are the closest wild relative of domestic horses. Left-side biases of approximately 57–68% were found in agonistic interactions, 63–73% in high alert and 53-54% in vigilance. As in other vertebrates, the right hemisphere of the horse is specialised to control agonistic interactions and responses to potential threats. Also consistent with previous research, showing right-hemisphere control of the expression of strong emotion, leftwards bias was stronger in measures of behaviour involving higher aggression and reactivity. Domestic riding horses were also studied using the same methodology and found to display leftside biases for the above measures, with the exception of vigilance, but the strength was weaker than in feral and Przewalski horses. This suggests (a) ancestral horses were more strongly lateralized for attack, vigilance and reactivity than are present-day domestic horses, and/or (b) lateralization is stronger in horses living in natural habitats. Limb preference, measured as the forelimb placed in front of the other during grazing, was investigated because previous research has shown limb preference in some breeds of domestic horse. No population bias of forelimb preference was found in feral or Przewalski horses or in most of the domestic horses studied, except Arab horses, which preferred to use the left forelimb as weight support during grazing (61%). This may reflect the flighty temperament of Arab horses since it suggests righthemisphere dominance. Stronger left-supporting limb preference was associated with increasing reactivity in feral horses. Stronger individual limb preferences were found in younger feral horses than in adult feral horses, indicating limb preference is modified by maturation or experience in the natural habitat. Side biases in threat, vigilance and reactivity are, apparently, also modified, by experience in the natural habitat or domestic environment, whereas side bias in attack is not. Domestic horses that had been ridden showed stronger biases in threat and reactivity than those that had never been ridden. The implications of these findings in regards to welfare are discussed.

CERTIFICATION

I certify that the substance of this thesis has not already been submitted for any degree and is not currently being submitted for any other degree or qualification.

I certify that any help received in preparing thesis and all sources used have been acknowledged in this thesis.



TABLE OF CONTENTS

CHAPTER 1 GENERAL INTRODUCTION

1.1	Introduction	1
1.2	Hemispheric specialisation	2
	1.2.1 Limb preferences	6
	1.2.2 Lateralization of eye use in viewing	8
	1.2.3 Lateralization of head-turning	11
1.3	Function of lateralization	12
	1.3.1 At the individual level	12
	1.3.2 At the population level	13

CHAPTER 2 LATERALIZATION IN DOMESTICATED ANIMALS AND ANIMAL WELFARE

2.1	Lateralized behaviour of large farm animals other than horses	14
2.2	Lateralized behaviour of domestic horses (<i>Equus caballus</i>)	16
2.3	Domestication	20
	2.3.1 Process of domestication	20
	2.3.2 Domestication of horses	21
2.4	Relevance of lateralization to the handling and management of	f farm animals 22
	2.4.1 Lateralization and safety	22
	2.4.2 Lateralization and welfare	23
	2.4.3 Lateralization and early experience	24
2.5	Research conducted for this thesis	25
	2.5.1 Feral horses (Equus caballus)	26
	2.5.2 Przewalski's horse (Equus ferus przewalski)	26
	2.5.3 Further research on domestic horses	27

CHAPTER 3 GENERAL METHODS

3.1	Intro	duction	29
3.2	Subje	cts and locations	30
	3.2.1	Feral horses	30
		3.2.1.1 Group 1	32
		3.2.1.2 Group 2	35
	3.2.2	Przewalski horses	38
	3.2.3	Domestic horses	40
	3.2.4	Observer effects	43
	3.2.5	Materials	44
		3.2.5.1 Equipment	44
3.3	Meth	ods	44
	3.3.1	Types of behaviour recorded	44
		3.3.1.1 Head-turning bias in vigilance, high alert and percentage	
		reactivity	45
		3.3.1.2 Eye preference during agonistic interactions	47
		3.3.1.3 Limb preference	51

3.4	Inter-rater reliability	52
3.5	Statistical analysis	53
	3.5.1 Laterality index	53
	3.5.2 G-test	53
	3.5.3 Other analyses	53
3.6	Ethical note	54

CHAPTER 4 FERAL HORSES PART 1

4.1		luction	55
4.2	Metho		56
	4.2.1	5	56
	4.2.2	Data collection	56
	4.2.3	Statistical analysis	57
4.3	Resul	ts	57
	4.3.1	Eye bias during agonistic interactions	57
		4.3.1.1 Within harem bands	57
		4.3.1.1.1 Age effects on laterality in agonistic responses	60
		4.3.1.2 Stallion fights	61
	4.3.2		63
		4.3.2.1 Laterality index in vigilance	63
		4.3.2.1.1 Effect of age on laterality in vigilance	64
		4.3.2.2 Percentage reactivity	65
		4.3.2.2.1 Age effect on percentage reactivity	66
		4.3.2.2.2 Effect of the type of stimulus on percentage reactivity	67
		4.3.2.3 Side bias in high alert	69
		4.3.2.3.1 Effect of age on laterality index in high alert	70
	433	Correlations between different measures of laterality	70
4.4	Discu		70
т.т	4.4.1		73
		Side bias in vigilance and reactivity	74
		Is laterality influenced by how long horses have been feral?	75
	4.4.4	Conclusion	76

CHAPTER 5 FERAL HORSES: PART 2 LIMB PREFERENCE

5.1	Introduction	77
5.2	Method	77
	5.2.1 Subjects and locations	77
	5.2.2 Data collection	77
	5.2.3 Statistical analysis	78
5.3	Results	
	5.3.1 Forelimb preference	78
	5.3.1.1 Effect of age on strength of laterality in limb preference	<i>nce</i> 81
	5.3.1.2 Stability in forelimb preference over time	82
	5.3.2 Correlation of limb preference with level of reactivity	82
	5.3.3 Correlation of limb preference with level of aggression	84
5.4	Discussion	
	5.4.1 Limb preference	84

Reactivity and limb preference	86
Conclusion	87

CHAPTER 6 PRZEWALSKI HORSES

6.1	Intro	luction	88
6.2	Meth	bd	89
	6.2.1	Subjects	89
	6.2.2	Data collection	89
	6.2.3	Statistical analysis	90
6.3	Resul	ts	90
	6.3.1	Eye preference during agonistic interactions	90
		6.3.1.1 Within harem bands	90
		6.3.1.2 Stallion fights	92
	6.3.2	<i>Comparison of left-eye bias between interactions within harem bands</i>	
		and those during stallion fights	94
	6.3.3	Side bias in vigilance	94
	6.3.4	Side bias in percent reactivity	95
	6.3.5	Side bias in high alert	96
	6.3.6	Forelimb preference	96
	6.3.7	Comparisons with feral horses	97
6.4	Discussion		98
	6.4.1	Eye preference in agonistic behaviour	98
	6.4.2	Side bias in vigilance and reactivity	100
	6.4.3	Limb preference	101
	6.4.4	Comparison of lateralization between Przewalski and feral horses	101
	6.4.5	Conclusion	102

CHAPTER 7 DOMESTIC HORSES

7.1	Intro	duction	103
7.2	Meth	ods	104
	7.2.1	Subjects	104
	7.2.2	Limb preference	105
	7.2.3		105
		Eye bias in agonistic behaviour	105
7.3	Resul		106
	7.3.1	Laterality in domestic horses	106
		7.3.1.1 Limb preference	106
		7.3.1.1.1 Case study on lameness and limb preference	109
		7.3.1.2 Side bias in vigilance	110
		7.3.1.3 Percentage reactivity	111
		7.3.1.4 Side bias in high alert	115
		7.3.1.5 Eye preference in agonistic interactions	116
	7.3.2		119
		7.3.2.1 Eye bias in agonistic responses	119
		7.3.2.2 Side bias in vigilance	121
		7.3.2.3 Percentage reactivity	122
		7.3.2.4 Side bias in high alert	122
		7.3.2.5 Limb preference	124

7.4	Discu	ission	124
	7.4.1	Differences between the Arab breed and other horses	125
		7.4.1.1 Limb preference	125
		7.4.1.2 Other side biases	127
	7.4.2	Effects of experience on laterality	127
		7.4.2.1 Side bias in reactivity	127
		7.4.2.2 Limb preference	129
		7.4.2.3 Eye preference in agonistic responses	130
	7.4.3	Conclusion	131

CHAPTER 8 GENERAL DISCUSSION

8.1	Introduction	133
8.2	Eye bias of agonistic responses	134
	8.2.1 Laterality in attack	136
	8.2.2 Laterality in threats	136
8.3	Side bias in vigilance and reactive responses	137
8.4	Limb preference	138
8.5	Lateralization in the natural habitat	140
8.6	Domestication	141
8.7	Implications for animal welfare	143
REF	ERENCES	146

LIST OF APPENDICES

Appendix I. Number of left and right scores per horse recorded by observing the feral horses: head-turning bias and eye preference.	166
Appendix II. Number of left and right scores per horse recorded by observing the Przewalski horses: all behavioural measures.	169
Appendix III. Number of left and right scores per horse recorded by observing the domestic horses: all behavioural measures.	171
Appendix IV. Comparison of 30- and 60-second-interval sampling data with scores of the percentage of time spent with the left forelimb in front of the right (%time = $L/(L+R)*100$)	175
Appendix V. Number of left and right scores per horse from the feral and Przewalski horses during stallion fights.	176
Appendix VI. Limb preference: Number of left and right scores per horse from the feral horses.	178

LIST OF FIGURES

Figure 2.1	Limb placements during grazing.	18
Figure 3.1	Locations of feral horse fieldwork sites in Australia.	31
Figure 3.2	Mona Mona Aboriginal Mission showing terrain and horses.	34
Figure 3.3	Oxley Wild Rivers National Park showing terrain and horses.	36
Figure 3.4	Takh Reserve at Le Villaret, France, showing terrain and Przewalski	
	horses.	39
Figure 3.5	Some of the domestic horses from North Queensland and the fields in	
	which they were housed	41
Figure 3.6	Arab horses and the terrain at the Center for Eco-Ethos Research and	
-	Education in France.	42
Figure 3.7	The heights to which horses raised their head to look at a stimulus.	46
Figure 3.8	An example of a horse with its ears pinned.	48
Figure 3.9	Two stallions boxing without contact being made.	49
Figure 3.10	Examples of agonistic interactions to illustrate the scoring method.	50
Figure 3.11	The stance adopted by the horse when grazing.	51
Figure 4.1	Scatterplot showing a funnel effect for 'threats'.	59
Figure 4.2	Frequency histograms of laterality indices for agonistic interactions	
	within harems.	60
Figure 4.3	The effect of age on strength of eye bias in threats and attacks.	61
Figure 4.4	Frequency histograms of laterality indices for agonistic interactions	
-	during stallion fights.	62
Figure 4.5	Comparison between harem and bachelor stallions of eye bias for	
	looking bouts containing threats only and looking bouts containing	
	attack during stallion fights.	63

Figure 4.6	Frequency histogram of laterality indices for vigilance.	64
Figure 4.7	The effect of age on strength of side bias in vigilance.	65
Figure 4.8	Levels of reactivity elicited by stimuli detected on the left side and on the right side.	66
Figure 4.9	Both immature and adult horses exhibit significantly higher levels of	
C	reactivity towards stimuli detected on the left than right side.	67
Figure 4.10	Level of reactivity shown by Group 1 and Group 2 horses when looking	
-	at either a conspecific or the observer detected on their left or right side.	68
Figure 4.11	Scatterplot showing a funnel effect for high alert.	69
Figure 4.12	Frequency histogram of laterality indices for high alert.	70
Figure 4.13	Scatterplots showing the relationships between side-bias in high alert	
	and eye-bias in threats.	71
Figure 4.14	Scatterplots showing the relationships between side-bias in high alert	
	and eye-bias in attack.	71
Figure 5.1	Scatterplot showing a funnel effect for limb preference.	79
Figure 5.2	Frequency histograms of laterality indices for forelimb preference	
	during grazing.	80
Figure 5.3	The effect of age on strength of limb preference.	81
Figure 5.4	Scatterplot showing the relationship between level of reactivity and	
	forelimb preference expressed as Laterality Indices.	82
Figure 5.5	Level of reactivity exhibited by horses that were significantly left-	
	forelimb and right-forelimb preferring.	83
Figure 5.6	Scatterplots showing the relationship between level of reactivity and	
	forelimb preference expressed as Laterality Indices.	83
Figure 6.1	The laterality index of all agonistic responses (threat plus attack) for	0.1
E	males compared to females.	91
Figure 6.2	Frequency histograms of laterality indices for agonistic interactions within harems.	91
Eiguro 6 2	The effect of age on strength of side bias in threats and attack.	91 92
Figure 6.3 Figure 6.4	Frequency histograms of laterality indices for agonistic interactions	92
Figure 0.4	during stallion fights.	93
Figure 6.5	Frequency histogram of laterality indices for vigilance.	95 95
Figure 6.6	The effect of age on the strength of bias for vigilance.	95 95
Figure 6.7	Frequency histograms of laterality indices for high alert.	96
Figure 6.8	Frequency histograms of laterality indices for forelimb preference	20
115010 0.0	while grazing.	97
Figure 7.1	Scatterplot of laterality index of forelimb preference during grazing	21
8	and the total number of scores obtained from each horse.	106
Figure 7.2	Histograms showing the population distributions of limb preference	
0	in purebred Arab horses and non-Arab (excluding crossbred Arab)	
	riding horses.	107
Figure 7.3	The effect of age and being ridden on the strength of limb preference.	109
Figure 7.4	Scatterplot of the relationship between laterality index for vigilance	
-	and the number of scores obtained for each horse.	110
Figure 7.5	Comparison between Arab and non-Arab horses of side bias in vigilance.	111
Figure 7.6	Population distributions of side bias in vigilance.	112
Figure 7.7	The percentage of high head lifts in order to look to the left or right.	112
Figure 7.8	Comparison of the percentage of head lifts above the level of the	
	withers for looks to the left and looks to the right between ridden and	
	non-ridden horses.	114

Figure 7.9	Comparison of the percentage of head lifts above the level of the	
	withers for looks to the left and looks to the right between non-Arab	
	recreational, purebred Arab and crossbred Arab riding horses.	114
Figure 7.10	Scatterplot of the relationship between laterality index for high alert	
	and the total number of scores.	115
Figure 7.11	Population distribution of LI scores for high alert shown by domestic	
	horses.	116
Figure 7.12	Comparison of the strength of side bias in high alert between immature	
C	and adult domestic horses.	116
Figure 7.13	Scatterplots of the relationships between the number of scores obtained	
	for each horse and laterality index for threats and attacks.	117
Figure 7.14	Population distributions of side bias for looking bouts consisting of	
	threats only and looking bouts containing at least one attack.	118
Figure 7.15	Comparison of the strength of side bias in agonistic looking bouts	
	containing threats and those containing at least one attack between non-	
	ridden and ridden domestic horses.	119
Figure 7.16	Mean side bias in threat in males and females of the three groups of	
e	horses.	120
Figure 7.17	Mean side bias in attack scores across the three groups of horses.	121
Figure 7.18	Comparison between groups of the percentage left-side difference	
e	scores in the percentage of head lifts that were above the wither level.	122
Figure 7.19	Mean side bias in high alert across the three groups of horses.	123

All photographic images were taken by the researcher while conducting fieldwork and used with permission of the owners or those responsible for management of the horses. Copyright was obtained from the appropriate authorities to adapt the topographical maps for use in this thesis (details are given under the maps).

LIST OF TABLES

Table 1.1	Summary of the main functions found to be lateralized in vertebrates.	3
Table 3.1	Field trip locations and dates.	33
Table 3.2	Agonistic responses recorded.	49
Table 4.1	Number of horses showing left or right LI-scores	70
Table 4.2	Summary of the findings on side biases in feral horses	72
Table 5.1	Number of horses showing left or right LI-scores	81
Table 5.2	Correlations between aggression and limb preference.	84
Table 6.1	The number of horses that displayed significant individual biases	
	for high alert, vigilance, and attack responses within harems.	98
Table 6.2	Strength of group biases and the percentage of individuals that	
	were significantly lateralized in Przewalski horses and feral horses.	101
Table 7.1	Limb bias in the different groups of domestic horses.	108
Table 7.2	The number of domestic horses that showed a significant individual	
	limb preference.	108
Table 7.3	Findings of side biases in feral horses, Przewalski horses and	
	domestic horses.	124
Table 8.1	Percentage of horses exhibiting significant individual lateralization.	142

GLOSSARY OF TERMS USED

Index of laterality: (Right scores – Left scores) / (Right scores + Left scores).

Laterality of vigilance: the number of times a horse stopped grazing and lifted and turned its head to the left and to the right. All head lifts, regardless of height of the lift, were included in this measure. These scores were used to calculate a laterality index (LI-vigilance).

Laterality of high alert: The number of times a horse stopped grazing and lifted its head to a height at which the poll was above the level of the withers when turning to the left or to the right. Note that this measure included only high head lifts because these are known to show elevated heart rate and activation of the sympathetic nervous system. A laterality index (LI-high alert) was calculated from these scores.

Percentage reactivity: The number of times a horse lifted its head with the poll above the level of the withers divided by the total number of times it lifted head to any height to look either to the left or to the right. If a horse lifted its head and looked leftwards 10 times and of these lifts five were above the level of the withers then percentage reactivity for left head turns would be 50%. A similar score was calculated for looks to the right. Percentage reactivity for left and right head turns was compared.

Level of reactivity: The number of times per hour that a horse stopped grazing and looked up, including left and right head turns as well as head lifts without turning of the head.

Looking bout: The period during which a horse fixated the head region of a conspecific using the left or right eye. This was scored only during agonistic interactions (threats or attacks).

Threat bout: A looking bout containing only low level threat responses (e.g. head threats, tail swishing, hindquarter movement, leg lifting). Often referred to simply as a threat.

Attack bout: A looking bout containing at least one high level threat response or attack (e.g. bite, kick, strike, rearing with contact or boxing, lunge, charge and chase). Often referred to simply as attack.

Laterality of threat: The number of threat bouts in which a horse fixated a conspecific with its left eye or with its right eye. A laterality index was calculated.

Laterality of attack: The number of attack bouts in which a horse fixated a conspecific with its left eye or with its right eye. A laterality index was calculated.

Level of aggression: The number of times per hour a horse engaged in an agonistic interaction (threat or attack).

Limb preference: The forelimb placed in front of the other during grazing measured using 30-second-interval sampling. Limb preference was calculated as a laterality index.

CONFERENCE PRESENTATIONS DURING CANDIDATURE

Austin, N. P. & Rogers, L. J. (2008). Side biases in domesticated and feral horses. *Proceedings* of the Australasian Society for the Study of Animal Behaviour, **35**, 18.

Austin, N. P. & Rogers, L. J. (2009). Side biases of feral horses: species-typical specializations. *Proceedings of the* 43rd *Congress of the International Society for Applied Ethology*, **43**, 406.

Austin, N. P. & Rogers, L. J. (2009). Species-typical side biases of horses. *Proceedings of the* 31st International Ethological Conference, **31**, 130.