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5
6 **Auditory laterality in a nocturnal, fossorial marsupial (*Lasiorhinus latifrons*) in**
7 **response to bilateral stimuli**

8
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16
17 Behavioural lateralisation is evident across most animal taxa, although few marsupial and
18 no fossorial species have been studied. Twelve wombats (*Lasiorhinus latifrons*) were
19 bilaterally presented with eight sounds from different contexts (threat, neutral, food) to
20 test for auditory laterality. Head turns were recorded prior to and immediately following
21 sound presentation. Behaviour was recorded for 150 seconds after presentation. Although
22 sound differentiation was evident by the amount of exploration, vigilance and grooming
23 performed after different sound types, this did not result in different patterns of head turn
24 direction. Similarly, left-right proportions of head turns, walking events and food
25 approaches in the post-sound period were comparable across sound types. A comparison
26 of head turns performed before and after sound showed a significant change in turn

27 direction ($\chi^2_1 = 10.65, P = 0.001$) from a left preference during the pre-sound period
28 (mean 58% left head turns, CI 49-66%) to a right preference in the post-sound (mean
29 43% left head turns, CI 40-45%). This provides evidence of a right auditory bias in
30 response to the presentation of the sound. This study therefore demonstrates that laterality
31 is evident in southern hairy-nosed wombats in response to a sound stimulus, although
32 side biases were not altered by sounds of varying context.

33

34 **Keywords**

35 Wombat; Behaviour; Laterality; Auditory; Marsupial

36

37 Lateralised behaviour is evident in many animal species, including humans (Vallortigara
38 & Rogers, 2005; Vallortigara, 2006; Corballis, 2007; MacNeilage, Rogers, Vallortigara,
39 2009), and is apparent in asymmetries of left-right cerebrum use, which manifests as a
40 side bias (Rogers, 2000). Its expression can be affected by task function, emotion and
41 perception, social structure, age or gender (de Latude, Demange, Bec, 2009; Pfannkuche,
42 Bouma, Groothuis, 2009). Laterality assists cognitive processing by reducing reaction
43 time (Rogers, 2000) and may enhance simultaneous performance of tasks that are
44 controlled by opposite hemispheres (e.g. feeding and vigilance) (Rogers, Zucca,
45 Vallortigara, 2004; Ghirlanda, Frasnelli, Vallortigara, 2009). At the population level,
46 laterality may aid social communication or predator avoidance strategies (Vallortigara,
47 Chiandetti, Sovrano, 2010).

48

49 Hemispheres appear to control different emotions and therefore the expression of
50 laterality has the potential to indicate the animal's perception of a stimulus (Rodriguez,
51 Gomez, Afonso, 1992; Hauser, 1993; Phillips, Llewellyn, Claudia, 2003; de Latude et al.,
52 2009). A review of lateralization by Rogers (2010) suggests that dominant use of the right

53 hemisphere may indicate an animal that is stressed or has a negative cognitive bias. The
54 orienting asymmetry paradigm is a non-invasive measure of auditory laterality, using
55 head turns in response to sounds of varied context (Hauser & Andersson, 1994; Teufel,
56 Ghazanfar, Fischer, 2010). In dogs (*Canis familiaris*) and Rhesus macaques (*Macaca*
57 *mulatta*) this test indicated that vocalisations from conspecifics that had been disturbed
58 by a stranger knocking at the door or isolated in a room were processed with the right ear
59 / left hemisphere (Hauser & Andersson, 1994; Siniscalchi, Quaranta, Rogers, 2008).
60 These stimuli did not represent an immediate and severe threat to the dogs. By contrast,
61 the left ear / right hemisphere was dominant in dogs for thunderstorm sounds and in
62 Rhesus macaques for heterospecific vocalizations”

63

64 Few marsupial species have been tested for laterality despite cerebral differences from
65 eutherian mammals (Lippolis, Westman, McAllan, Rogers, 2005). Similar to birds,
66 marsupials lack a corpus callosum, which bridges the hemispheres and may play a role in
67 lateralisation (Wiltschko, Traudt, Güntürkün, Prior, Wiltschko, 2002; Josse, Mohamed,
68 Kherif, Price, 2008), although they do possess an anterior commissure, which
69 interconnects the auditory fields of the hemispheres (Heath & Jones, 1971; Aitken, 1995).
70 Unlike marsupials, lateralisation in birds has been extensively studied and the patterns of
71 hemispheric use are similar to mammals (Rogers, 2008). The wombat presents a useful
72 marsupial model for such studies due to its laterally placed eyes (Sanderson & Pearson,
73 1981), largely immobile ears, and its nocturnal, semi-fossorial behaviour. This study
74 aimed to determine whether wombats are lateralised in their response to auditory stimuli,
75 and whether this is influenced by sound type and context.

76

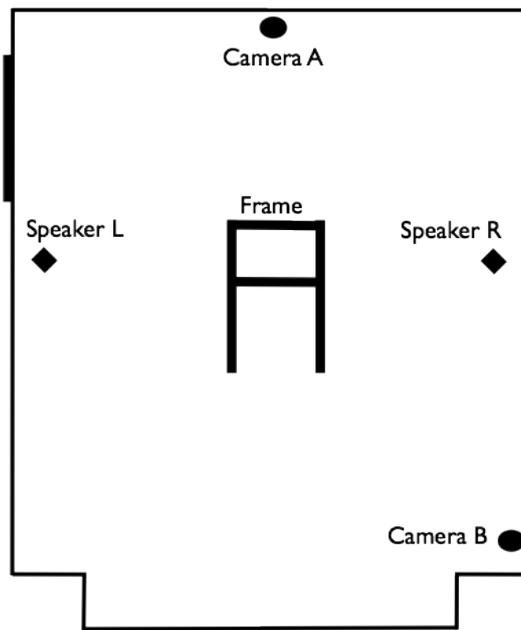
77

77 **Methods**

78 This study used twelve adult southern hairy-nosed wombats (*Lasiorhinus latifrons*)
79 maintained in four groups of one male with two females. Eleven of these were collected
80 from the wild 5 - 8 years prior to this study and one was born at the facility in 2003. Each
81 group was provided with a temperature-controlled burrow system, digging chamber,
82 feeding house, log and an outside enclosure (76 m² - 249 m²) with native grasses. Carrots,
83 hay and macropod pellets were provided daily. The wombats were checked during
84 routine cleaning and weighed fortnightly. Ethical clearance was obtained from the
85 University of Queensland, Animal Ethics Committee (licence number: SAS/402/09).

86

87 Audio testing occurred in a vacant den (Figure 1) identical to those used by the wombats.
88 A wooden and wire mesh feeding frame was placed centrally to control the wombat's
89 position, and two speakers (Logitech, LS11, Dick Smith Electronics) were attached
90 bilaterally (azimuth = 90° and 270°) to the den roof. Two infrared cameras (Sony IR
91 Outdoor Night Vision CCIR 507L28) and surveillance software (Skyview Super-series,
92 Skyview) were used to record behaviour at two frames per second in black and white.
93 Wombats were habituated to the equipment to avoid confounding results from neophobia
94 (Robins & Phillips, 2009).



95

96 *Figure 1: Two-dimensional representation of the test den.*

97

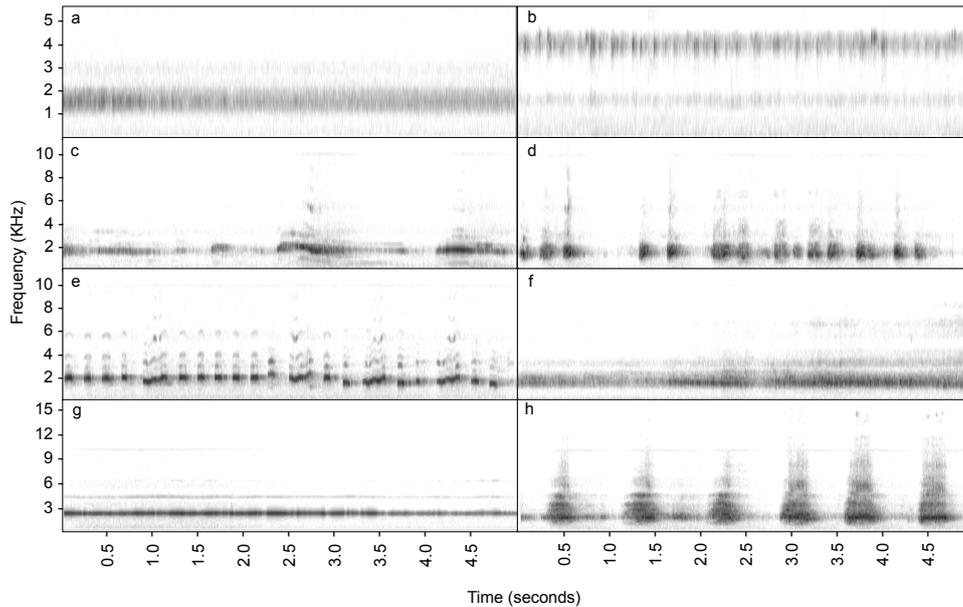
98 *Treatment sounds*

99 Eight sound clips were used from three different contexts – threat, neutral and food-
 100 conditioned. Wombat hissing, and vocalisations from two predators (dog and dingo) were
 101 used as threatening sounds. Two sounds believed to be neutral (air-conditioning and
 102 aeroplane), were chosen because they were heard frequently at the test site without
 103 evoking behavioural responses from the wombats. Three novel and biologically irrelevant
 104 sounds (bells, opera and whistle) were positively conditioned to a food reward by
 105 offering a preferred treat immediately after presenting the sound. This was done six times
 106 per day for five days prior to testing.

107

108 All sound files were monophonic and five seconds in length, with a median volume of 62
 109 - 67.5 dB SPL (Digital Sound Level Meter, Q1362, Dick Smith Electronics). The sound
 110 pressure level produced by each speaker was identical (mean difference in minimum level
 111 across 8 sounds was 0 dB SPL and maximum level was 0.5 dB SPL). Frequencies were

112 analysed using Raven Pro (version 1.3) spectral analysis software (Figure 2).
113 Spectrogram frequency outputs from the two speakers were compared and found to be
114 less variable than output from the same speaker played two times (mean cross
115 correlations for eight sounds was 0.958 for within speaker variation, compared with 0.971
116 for between speakers).
117



118
119 *Figure 2: Spectrograms (Raven Pro, version 1.3) of eight test sounds: a) Air-*
120 *conditioning, b) Bells, c) Dingo, d) Dog, e) Opera, f) Plane, g) Whistle, h) Wombat.*
121 *Sounds a, b, g and h were recorded on-site using a digital audio recorder (Joybee 110,*
122 *BenQ). Sounds c - f were sourced from soundboard.com.*
123
124 Testing began at 0600 h, and was carried out in three blocks of 9, 9 and 6 days, with four
125 wombats tested individually and in a random order each day. Testing lasted between 566
126 - 3612 seconds, and all wombats had an inter-test rest period of 3 days.
127

128 Behaviour was recorded over three periods: baseline (head turns prior to sound
129 presentation), response (head turns within 30 seconds of sound presentation) and post-
130 sound (all behaviour within 150 seconds of sound presentation). One trained observer
131 scored all of the video data, and a second trained observer scored 5 % of the videos to
132 check for inter-rater reliability (94.9 %). Behaviour was categorised into head turns
133 (vigilance), feeding, locomotion, escape, exploration, resting and grooming. Food was
134 placed into the bowl using a reaching tool (Nifty Nabber, Crafright) through a hole in the
135 roof that also allowed discrete viewing of the den. The sound was presented once the
136 animal was in the feeding frame with its head straight and of equal distance between the
137 two speakers. Responses were considered invalid if the sound played when these criteria
138 were not met. The procedure was repeated twice more using the same sound. Wombats
139 that did not approach the bowl within three minutes (16 % occurrence) were lured to it
140 using the reaching tool. On two occasions luring did not work within 20 min and the
141 wombat was released back into its enclosure and re-tested at the end of the session.

142

143 *Statistical analysis*

144 *Head turn in response to sound*

145 The direction of responsive head turns was analysed for the effect of sound type using
146 Chi-square tests of associations (Freq procedure, SAS®, version 8.2) for left and right
147 turns, and no response. Head turn preferences for individuals and after each sound type
148 were calculated using an Exact Binomial Test, using only responses in which a left or
149 right choice had been made.

150

151 *Behaviour post-sound*

152 Post-sound behaviour (0 – 150 seconds) was categorised into feeding, locomotion,
153 vigilance, escape, exploratory, resting and grooming. Data were not normally distributed

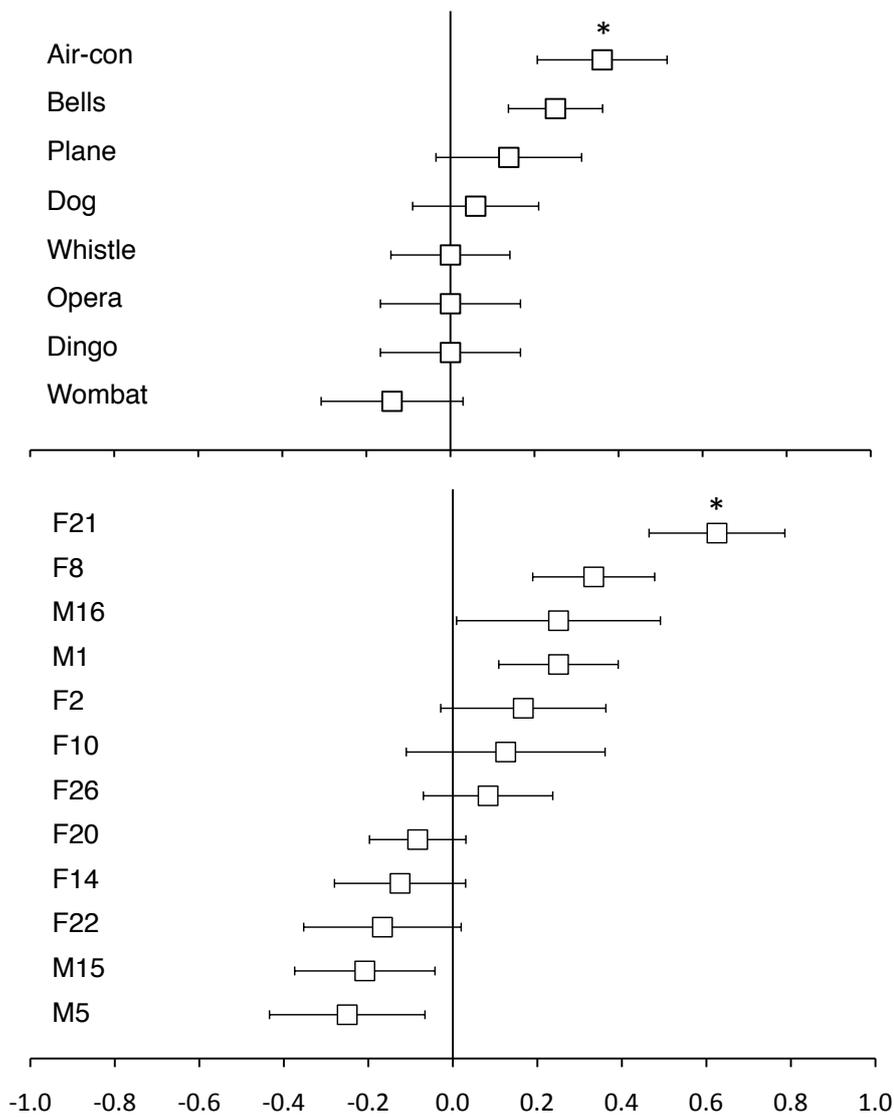
154 by univariate analysis, therefore behavioural frequencies were analysed using a Genmod
155 procedure with a Poisson distribution in SAS to determine the influence of sound type.
156 Resting was too infrequent to include. If an overall effect of sound was indicated, post-
157 hoc Chi-square tests were conducted to test for differences in behaviour between sounds.
158 Three post-sound behaviours were directional: walking (clockwise/anti-clockwise), head
159 turns (left/right) and food approach (bowl on left/right). These were analysed using the
160 Genmod procedure in SAS with a binomial distribution to determine whether sound type
161 influenced direction. Pre- and post-sound data were compared using the Genmod
162 procedure with a binomial distribution in SAS.

163

164 **Results**

165 The direction of responsive head turns was not influenced by sound type ($\chi^2_{14} = 14.24$, P
166 $= 0.43$), although one sound (air-conditioning) was significantly skewed to the right
167 (Figure 3). Only one individual had a significant directional preference (Figure 3). The
168 direction of post-sound walking, head turning or food approach was similar between
169 sounds (Table 1). Head turn direction significantly changed ($\chi^2_1 = 10.65$, $P = 0.001$) from
170 a left preference [proportion left (with 95% CI) = 0.58 (0.49 – 0.66)] in the baseline
171 period to a right preference in the post-sound period [proportion left (with 95% CI) =
172 0.43 (0.40 – 0.45)]. This change was not affected by the type of sound presented ($\chi^2_7 =$
173 6.77, $P = 0.45$) (Table 2).

174



175

176 *Figure 3. Mean head turn preferences (\pm SE) for individual wombats and sounds.*

177 *Negative and positive means indicate a left and right preference respectively. Preferences*

178 *were calculated by attributing a left response with -1, right response with +1 and no*

179 *response with 0 then calculating means for each individual or sound. * indicates a*

180 *significant ($p < 0.05$) preference using an Exact Binomial Test.*

181

182

182 **Table 1. Back-transformed proportions (with 95% CI) of left or anti-clockwise**
 183 **behaviour after 8 sound types, and the overall sound effect on direction (χ^2 statistic,**
 184 **degrees of freedom, probability value).**

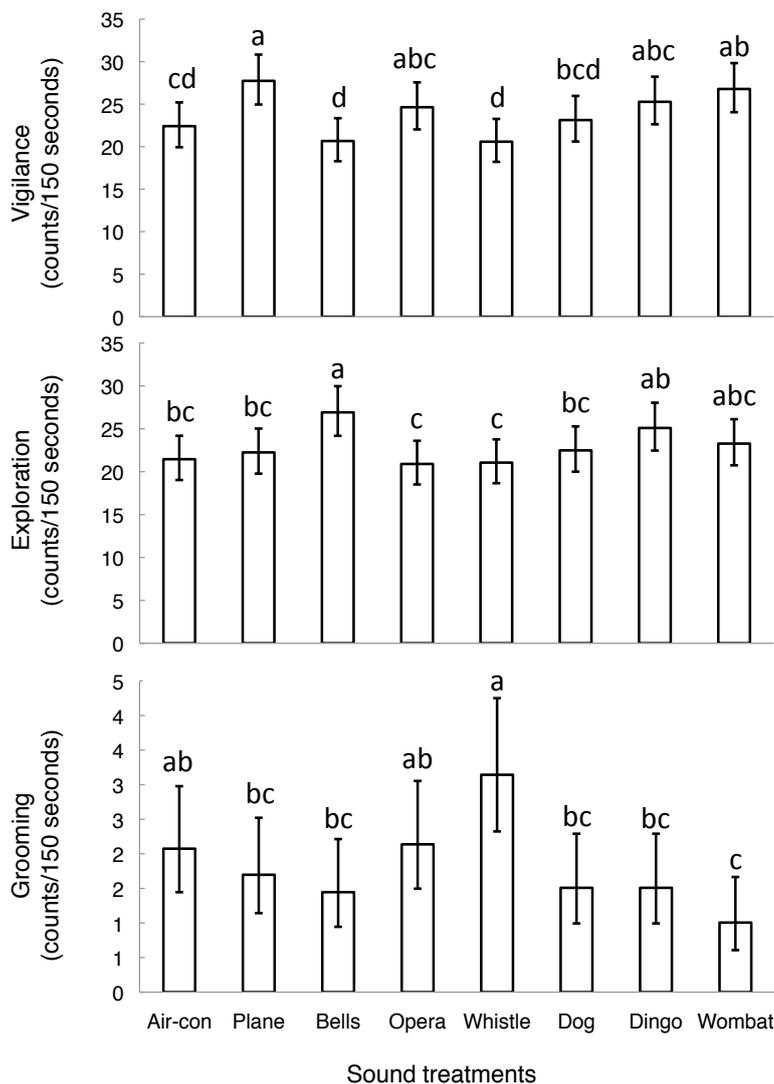
| Sound type | Head movement left | Approach food left | Walking anti-clockwise |
|--------------|-----------------------------|-----------------------------|------------------------------|
| Air-con. | 0.40 (0.32 – 0.47) | 0.55 (0.28 – 0.79) | 0.65 (0.56 – 0.72) |
| Bells | 0.40 (0.33 – 0.48) | 0.52 (0.27 – 0.76) | 0.60 (0.51 – 0.67) |
| Dingo | 0.46 (0.39 – 0.53) | 0.66 (0.43 – 0.83) | 0.57 (0.49 – 0.64) |
| Dog | 0.41 (0.34 – 0.49) | 0.61 (0.35 – 0.82) | 0.66 (0.58 – 0.73) |
| Opera | 0.45 (0.38 – 0.52) | 0.46 (0.22 – 0.73) | 0.61 (0.52 – 0.69) |
| Plane | 0.39 (0.32 – 0.46) | 0.49 (0.25 – 0.73) | 0.66 (0.58 – 0.73) |
| Whistle | 0.44 (0.37 – 0.52) | 0.39 (0.18 – 0.65) | 0.71 (0.63 – 0.78) |
| Wombat | 0.47 (0.40 – 0.54) | 0.64 (0.41 – 0.82) | 0.68 (0.61 – 0.75) |
| Sound effect | $\chi^2_7 = 5.37, p = 0.62$ | $\chi^2_7 = 3.81, p = 0.80$ | $\chi^2_7 = 10.61, p = 0.16$ |

185

186 **Table 2. Back-transformed proportions (with 95% CI) of left head turns after 8**
 187 **sound types.**

| Sound type | Proportion left pre-sound | Proportion left post-sound |
|------------|---------------------------|----------------------------|
| Air-con. | 0.47 (0.27 – 0.69) | 0.40 (0.32 – 0.47) |
| Bells | 0.72 (0.43 – 0.89) | 0.41 (0.33 – 0.49) |
| Dingo | 0.55 (0.31 – 0.78) | 0.46 (0.39 – 0.53) |
| Dog | 0.37 (0.19 – 0.61) | 0.41 (0.34 – 0.49) |
| Opera | 0.60 (0.46 – 0.73) | 0.45 (0.38 – 0.52) |
| Plane | 0.74 (0.44 – 0.92) | 0.38 (0.32 – 0.46) |
| Whistle | 0.51 (0.33 – 0.68) | 0.44 (0.37 – 0.52) |
| Wombat | 0.60 (0.35 – 0.81) | 0.47 (0.40 – 0.81) |

188 Sound type significantly affected the expression of three behaviours in the post-sound
 189 period: exploration ($\chi^2_7 = 16.8, p = 0.02$), vigilance ($\chi^2_7 = 26.2, p = 0.0005$) and grooming
 190 behaviour ($\chi^2_7 = 24.1, p = 0.001$) (Figure 4). Vigilance behaviour was exhibited most
 191 frequently after the plane and wombat sounds and least frequently for bells and whistles.
 192 Exploratory behaviour occurred most commonly after hearing bells, while the whistle
 193 elicited the most grooming and the wombat the least.
 194



195
 196 *Figure 4. Mean counts (± 95% CI) of vigilance, exploration and grooming after the*
 197 *presentation of eight sound types. Means with different letters are significantly different*
 198 *($p < 0.05$).*

199 **Discussion**

200 It is evident that the wombats could distinguish between different sounds, as the amount
201 of vigilance, exploration and grooming was significantly affected by sound type.

202 Vigilance was performed most frequently after plane and wombat sounds and least after
203 whistles and bells. Wombat hissing represents a threat, while the whistle and bells were
204 conditioned to food and therefore these results are mostly unsurprising. The plane sound,
205 however, was believed to be neutral due to its frequency in the test vicinity and usual lack
206 of response by the wombats. The higher amount of vigilance shown after this sound
207 suggests that threat perception was influenced by context (Thorson, Morgan, Brown,
208 Norman, 1998), and habituated sounds encouraged alertness when they were presented in
209 a novel setting. Grooming was infrequent after all agonistic sounds (wombat, dog, dingo),
210 which is probably because threatened animals direct less energy towards maintenance
211 behaviour such as scratching (Hirsch, 2002; Stojan-Dolar & Heymann, 2010).

212 Differences in exploration and grooming were apparent between food-conditioned
213 sounds, indicating that conditioned responses may be affected by sound type. Despite
214 sound differentiation, wombats did not demonstrate lateralised behavioural responses to
215 sounds of varying context. No side preferences were evident for responsive head turns or
216 post-sound directional behaviour, a result that concurs with Fischer et al.'s (2009)
217 orienting study in humans.

218

219 Exposure to sound of any type significantly changed the direction of head turns from a
220 left bias in the baseline period to a right bias after sound presentation. This may be due to
221 a right auditory bias, as seen in humans (Tallus, Hugdahl, Alho, Medvedev, Hämäläinen,
222 2007; Devlin, Raley, Tunbridge, Lanary, Floyer-Lea, et al. 2003), which becomes
223 strengthened after sound presentation due to increased focus on that side (Tallus et al.,
224 2007). Alternatively the change may result from habituation to the test situation with the

225 wombats displaying vigilance (left side) on first entering the den, and then switching to
226 the right as they become familiar with the environment. This would concur with previous
227 studies that show most species (60 – 95%) exhibit a right hemisphere / left side
228 preference for vigilance (Vallortigara & Rogers, 2005), while familiar objects are usually
229 processed by the left hemisphere / right side (Robins & Phillips, 2009). Speaker
230 differences may also have influenced the change in head turn, as speaker positions were
231 not randomised. However, this is unlikely as turn direction changed significantly while
232 measured differences between speakers were minimal, and discrepancies would need to
233 be consistently in the same direction to have caused this change.

234

235 This study concludes that the southern hairy-nosed wombats exhibited lateralised
236 behaviour in response to sound presentation, although the expression was unaffected by
237 different types of auditory stimuli. Further studies using this species are recommended to
238 clarify the functional drivers of this hemispheric specialisation in marsupials.

239

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243 accommodation at the Rockhampton Botanic Gardens and Zoo. Technical support and
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