Whisker touch guides canopy exploration in a nocturnal, arboreal rodent, the Hazel dormouse (*Muscardinus avellanarius*)

Kendra Arkley[1], Guuske P Tiktak[2], Vicki Breakell[3], Tony J Prescott[1] & Robyn A Grant[2*]

1. Active Touch Laboratory, Department of Psychology, University of Sheffield, Sheffield, UK
2. Conservation Evolution and Behaviour Research Group, Division of Biology and Conservation Ecology, Manchester Metropolitan University, Manchester, UK
3. Wildwood Trust, Herne Common, Kent, UK

* Corresponding author:
Division of Biology and Conservation Ecology, Manchester Metropolitan University, Chester Street, Manchester, M1 5GD.
Email: robyn.grant@mmu.ac.uk
Tel: +44 (0)161 2476210

Acknowledgements

The authors would like to thank Hazel Ryan for her continued help and support, especially in handling the dormice; also to Hazel Ryan and Angus Carpenter for their comments on the manuscript. We are extremely thankful to the Wildwood Trust for the use of their facilities and animals. The authors are also grateful to Ben Mitchinson for designing the climbing arenas and developing the portable set-up, and to Holly Langridge and Fraser Combe for data collection support. Thanks to Brendan O'Connor for finding and translating some of the literature. Video analysis was performed using the BIOTACT Whisker Tracking Tool which was created under the auspices of the FET Proactive project FP7 BIOTACT project (ICT 215910), which also partly funded the study, alongside a small project grant from the British Ecological Society (BES). A big thanks goes to the CEB Research Group at MMU for listening to results summaries and advising about the project direction.

Abstract

Dormouse numbers are declining in the UK due to habitat loss and fragmentation. Dormice are nocturnal, arboreal, and avoid crossing open spaces between habitats, yet how they navigate around their canopy is unknown. As other rodents use whisker touch sensing to navigate and explore their environment, we investigate whether Hazel dormice (*Muscardinus avellanarius*) employ their whiskers to cross between habitats. We analysed high-speed videos of dormice exploring freely in flat and climbing arenas in near darkness using infrared light illumination. We confirm that, like rats and mice, dormice move their whiskers back and forth continuously (~10 Hz) in a motion called whisking and recruit them to explore small gaps (<10 cm) by increasing the amplitude and frequency of whisking, and the asymmetry of movement between the left and right whisker fields. When gaps between platforms are larger than 10-15 cm dormice spend more time travelling on the floor. These findings suggest that dormice can *actively* and purposively move their whiskers to gather relevant information from their canopy at night. As this species is vulnerable to threats on the ground, we also provide evidence that joining habitat patches between dormouse populations is important for promoting natural behaviours and movement between patches.

* 5 key words
whisker; vibrissa; active touch sensing; dormouse; climbing

Introduction

The Hazel Dormouse (*Muscardinus avellanarius*) is an arboreal and nocturnal habitat specialist (see **Fig. 1a** for an image). It lives almost exclusively in trees and actively avoids the ground and open spaces by travelling through the tree canopy around habitat gaps (Bright and Morris 1991; 1992; Morris 2003). There has been a marked decline in dormouse numbers in the UK due to habitat loss, isolation and fragmentation (Mortelliti et al. 2011; Ramakers et al. 2014), and so increasing these diminishing dormouse populations by connecting suitable habitat patches – for instance by building habitat corridors and dormouse bridges (Stride 2009) – is critical to this species' survival. Dormice are usually found in woodlands that are well connected to hedgerows (habitat "corridors"), and are almost entirely absent in regions without (Bright et al. 1994). Hedgerows, in particular, can be used as dispersal routes and are thus associated with immigration and recolonization within empty habitat patches (Bright and Morris 1996), however, they have to be extremely well connected as dormice are averse to descending from the canopy in order to bridge gaps (Bright 1998).

Dormice of the species *Glis glis* have been observed jumping distances of up to 40 cm (Kahmann and Ostermann 1951). These animals are capable of crossing greater distances, however, as Bright (1998) demonstrated, larger distances (>1 m in this study) involve crossing on the floor – with only 6% of approaches to smaller (1-3 m) gaps being completed, and 6 m gaps never being crossed. In a translocation study, Mortelliti et al. (2013) found large individual differences in gap crossing, with some Hazel dormice being capable of travelling over open fields of up to 106 metres in as little as one day; however, they often stayed for up to 18 days before crossing to their original (or a new) habitat patch. In this sample 30% of translocated dormice opted to stay in their habitat patch for the entire study duration. Notwithstanding these differences, it is likely that hedgerow gaps significantly reduce movement between habitat patches, and understanding how dormice cross between habitat gaps and navigate their canopy is an important first step in understanding how to manage their populations.

Little is known about the biology, sensory ecology, or behaviour of the Hazel dormouse due to its status as a protected species in the UK, its shy, arboreal, and nocturnal nature (Berg and Berg, 1999), and the large period of the year they spend in hibernation (Bright et al. 2006). Nevertheless, it is argued that the most highly developed sense in dormice is that of touch (Grzimek et al. 2004). When crossing between platforms in the dark, three blind dormouse species (species not specified) only jumped when they were close enough to touch with their whiskers (Airapet'yants 1974, as cited in Thomas et al. 2004), suggesting that whiskers are essential for gap crossing. However, it is probable that (like other rodents) hearing, vision and smell also play a role in guiding orientation around their arboreal environments. Dormouse hearing is sensitive up to 60 kHz – a similar range to rats and harvest mice (Thomas et al. 2004) – and their eyes are relatively large to compensate for low light levels (Grzimek et al. 2004). Non-tactile cues (e.g. echolocation, vision) are likely to be recruited to jump gaps greater than the whisker span when available (e.g. in *Glis glis* [Kahmann and Ostermann 1951]).

Given the limited body of research examining dormouse behaviour and biology, it is necessary to use insights from other nocturnal arboreal rodents, such as mice and rats, to theorise about how these animals explore their environments in darkness. Mice and rats are competent climbers and possess good grasping skills (Schmidt and Fischer 2010) that are thought to be guided by a combination of olfactory, visual and tactile cues (Bhattacharyya and Bhalla 2015; Niederschuh et al. 2015; Schroeder and Ritt 2016). However, the tactile whisker sense plays a primary role in environmental exploration and locomotion in both rats and mice (Vincent 1912; Watson 1907). Certainly, rodents adapt whisker positions and movements according to running speed and footfalls, and to detect obstacles (Arkley et al. 2014; Niederschuh et al. 2015). In addition, while rodents jump across very large gaps during the day using visual cues (Goodale et al. 1990; Legg and Lambert 1990; Wallace et al. 2013), when crossing small gaps (or in the dark) they recruit their whiskers, fully protracting them to touch the other platform before crossing (Jenkinson and Glickstein 2000).

The whiskers of rats and mice move in a cyclic motion called *whisking*, which is amongst the fastest movements that mammals can make, at a frequency of up to 25 Hz in mice (Mitchinson et al. 2011; Grant and Arkley 2015). The kinematics of whisker movements can be related to the facial musculature of animals. Extensive studies in mice and rats have revealed that they possess three groups of whisking muscles (Haidarliu et al., 2010). The *protracting muscles* are intrinsic to the mystacial pad and cause the whiskers to move forwards and backwards in the *rostrocaudal* (RC) plane and rotate torsionally within the follicle (Knutsen & Ahisssar 2008). These intrinsic muscles are largely conserved in mammals, and have been identified in marsupials (Grant et al. 2013), rodents (Haidarliu et al. 2010; Grant et al. 2016), and even nocturnal primates (Muchlinski et al. 2013). *Retracting muscles* that are extrinsic to the mystacial pad translate the whisker pad caudally in order to cause a retraction of the whisker field (Haidarliu et al. 2010; 2015). *Vertical-moving muscles* translate the pad vertically in the *dorsoventral* (DV) plane, causing the more dorsal whiskers to occupy and maintain a more vertical, dorsal position (Haidarliu et al. 2015). Knutsen and Ahissar (2008) studied 3D whisking kinematics and found that whisker movements in the RC, DV and rotational planes are tightly coupled, such that movement in the RC plane provides a good summary measure of the overall movement of the whisker.

The aim of this study is to provide the first characterisation of active whisker sensing in the Hazel dormouse (*Muscardinus avellanarius*). Due to the impact of habitat connectedness on species survival, we focus on whisker touch sensing during locomotion and gap crossing. First, we compare dormouse whisker movements in the RC plane, by filming in a top-down view (see **Fig. 1b**), with those of rats and mice during freely-moving behaviour on a flat floor. Second, we examine movement in the DV plane by recording in a side-on view (**Fig. 1c**), during forward locomotion on flat and sloping substrates, and during exploration of gaps. Third, we investigate gap-crossing behaviour for a range of gap sizes. We predict that if dormice use their whiskers in a similar way to other rodents, then we might expect them to be employed to guide locomotion in the dark, and during gap exploration in order to ensure a safe crossing.

Methods

Animals

Eight adult hazel dormice (*Muscardinus avellanarius*) were used in this study (four female and four male), aged from six weeks to ~two years. Animals were filmed in a flat floor arena and/or a climbing arena (**Fig. 1**). All animals were part of a rescue and rehabilitation program, or from a breeding pool at the Wildwood Trust in Kent, UK. All experiments were carried out at the

Wildwood Trust during the day (10.00-16.30), in semi-darkness in an on-site research facility. All experiments were approved by local ethics committees at each of the academic institutions and at the Wildwood Trust.

High-speed video analysis of dormice in the flat floor arena

Six dormice were included in this part of the study (two female and four male). Sixty high-speed videos were recorded in near-darkness using a Photron Fastcam (500 frames per second, 1024×1024 resolution) positioned above the flat floor arena (**Fig. 1b**). To yield a silhouette of the animal including its whiskers from a top-down view, the arena sat on a custom-built, infrared LED light box. The experimental arena (30x20x15 cm) had a lightly textured clear Perspex floor, so that the dormice could locomote easily. Handling of the dormice was kept to a minimum, and only by certified handlers, with a cardboard tube used to feed the animals into the arena. The dormice exited the tube and were allowed to freely explore the arena. Whilst exploring, several 1.6s video clips were recorded opportunistically (by manual trigger) when the animal moved beneath the field of view of the camera. Animals were filmed on two to three consecutive days, generating around ten clips per animal.

Four to six clips from each mouse in the *top-down* view were selected for analysis, or portions thereof, using the following selection criteria developed in Grant et al. (2013): i) the dormouse was clearly in frame; ii) both sides of the face were visible; iii) the head was level with the floor (with no extreme pitch or yaw); iv) the whiskers were not in contact with a wall; and v) the dormouse was clearly moving forward. In each selected clip, the snout and whiskers of the dormouse were tracked using the BIOTACT Whisker Tracking Tool (BWTT; Perkon et al. 2011) that semi-automatically detects and tracks the contours of the snout and all available whiskers. Due to debris in the arena, three video clips were manually tracked as in Grant et al. (2009) using a custom-built manual whisker annotator (Hewitt et al. 2016). From this method we were able to estimate, in each frame, the position of the snout tip and of a centre point along the midline of the head, and a set of estimated whisker base angles indicating whisker RC angular positions relative to the midline of the snout (**Fig. 1b**, bottom panel). Tracking was validated by manually inspecting the tracking annotation overlaid on to the video frames, with poor tracking removed prior to analysis. A total of thirty video clips (each ~0.5 s long), were included in the *flat floor* analysis. For each selected video clip or portion thereof, we computed the mean angle of the whiskers on each side of the snout calculated as the average of the measured angular positions of all identified whiskers (θ^{RC}). For each whisker field we estimated the *set point*, *asymmetry*, *amplitude* and *frequency* of whisker movements in the RC plane as follows. *RC Set point* was calculated by taking the mean whisker angle across all tracked frames. RC *asymmetry* was calculated by comparing the difference in angular position between the left and right sides and averaging over the entire clip. The *RC amplitude* was calculated by taking the root mean square across all tracked frames. To calculate *RC* whisk *frequency*, a measure of whisk power was first calculated by taking the average power spectral density (PSD) within the range of 4-50 Hz using the Fourier transform, before taking the centre of mass (average frequency weighted by power) of these computed PSDs. To obtain a single summary value for each trial from the left and right whisker fields, we took the mean across the two sides; it is these per-trial summary values that are presented in the results. *Locomotion speed* was also estimated in cm/s using snout-tip coordinates.

High-speed video analysis of dormice in the climbing arena

Five dormice were used in this part of the study (two male and three female). Animals were introduced to the climbing arena (35x20x45 cm, **Fig. 1c**) and housed inside individually for 2 weeks prior to filming. The floor of the arena contained a nest box, food bowl and water bowl. Sloping and flat poles (one-centimetre diameter dowels wrapped in twine) were fixed within the arena so that the dormice could climb a slope to two food platforms at the top of the arena, containing fresh cut fruit. The flat pole could be moved away from one platform to make a gap. Additional hazel branches were added to the arena to promote exploration and climbing. Each dormouse was filmed in the climbing arena over two consecutive days in near darkness. At the beginning of filming, the dormice were removed from their nest box and placed on one of the food platforms, with the nest box entrance blocked during the entire filming session.

A total of 51 video clips were collected opportunistically from a side-on view (**Fig. 1c**) as dormice moved along a flat pole, a sloped pole or exploring a gap. The flat pole was moved to enable a four-centimetre gap for the dormice to explore and cross within the arena. A *flat substrate* was defined as a pole, branch or food platform that was entirely parallel to the floor of the arena. A *sloped substrate* was a pole or branch that was inclined to ~45°. An analysis of inclined and declined slopes did not yield significant differences, therefore this surface type included video clips of dormice moving up and down the surface, either on top or underneath. *Gap exploration* was defined as the dormice extending and exploring into space: this usually involved exploring the gap in front of the food platform (**1**), but could also include exploring other open spaces in the canopy (such as in **Fig. 2b** and **Fig. 6c**). For all of these instances, video clips were selected for *side-on* snout and whisker tracking using the BWTT using the following criteria: i) the head was side-on to the camera ii) the snout tip and head were visible and iii) the most dorsal whiskers could be clearly seen. After validation of the tracking by manual inspection, a total of 34 clips were included in the analysis (*flat substrate* = 15, *sloping substrate* = 14, *gap exploration* = 5). In the five gap exploration clips, we also calculated the maximum length from the most rostrally placed forepaw to the most extended whisker tip, to give an approximation of *whisker reach*, using the manual tracking program Tracker (Brown 2015). Due to the variable nature of gap exploration, dormice did not always position their head side-on to the camera, which accounts for the lower number of video clips. However, an additional six video clips of gap exploration were tracked in the *top-down* view (**Fig. 2b**), yielding the same view as in the flat floor arena (**Fig. 2a**). For side-on clips, the most ventral whiskers were frequently contacting the floor during locomotion and often obscured; therefore, only the dorsal-most whiskers were tracked and included in the analysis – defined as those above the midline of the snout (**Fig. 1c**, bottom panel). We calculated the locomotion speed, set-point, amplitude and frequency of whisker movements in the DV plane (referred to as *DV set-point*, *DV amplitude* and *DV frequency*) as in the RC whisker analyses, but using the dorsal-most mean angular position only (θ^{DV}).

Five example video clips were also manually tracked to show an example of walking on a flat substrate, a sloped substrate, exploring a gap, and crossing a gap and jumping (**Fig. 4** and **Fig. 6**). Four points were tracked over 200 milliseconds in each clip using a custom-built manual whisker annotator (Hewitt et al. 2016); this included three whisker tips (a ventral, midline, and dorsal whisker) and the snout tip. The coordinate points of this tracking were overlaid onto video stills of the first tracked frame in **Fig. 4** and **Fig. 6**.

Camera trap of general behaviours

Four animals were reused from the climbing arena experiment (three female and one male). Following high-speed video recording, the animals continued to be housed in the climbing arena. Each night the flat substrate (a platform containing fresh cut fruit to encourage gap crossing) in the climbing arena was moved to make the gap bigger (**Fig. 1d**). The gap was increased by five-centimetres each night if the gap was successfully crossed, up to 25-28 cm (the limit of the arena). If a crossing did not occur, the gap was reduced by five-centimetres, and then increased by one-centimetre each night. A successful crossing was confirmed using i) examination of videos from a Bushnell HD infrared camera trap positioned above the gap (**Figure 1d**, bottom panel). Each night the dormice were filmed between 17:00-08:00, with recordings of ten seconds (with a ten second interval period) being triggered by movement and heat; ii) inspection of plain white paper on both sides of the gap for droppings and footprints.

As well as providing a record of gap crossings, the camera trap video footage for two animals was also inspected for general behaviours. The position of the dormouse within the arena was recorded in each video clip (the ground, branches/poles [flat/sloped substrates], food platform, and mesh ceiling of the arena). In addition, each video clip from the camera trap was scored to include the frequency of *walking*, *jumping*, *climbing*, *eating fruit*, *staying still*, *searching,* and *grooming*. *Walking* was defined as travelling with at least two limbs remaining on the floor, whereas *jumping* was defined as all limbs leaving the floor. *Climbing* involved walking on a surface angled at ~45°. *Eating* was recorded when the dormouse nosed in the food bowl or fruit platform, and had clear accompanying chewing motions. *Staying still* was verified when the dormouse was entirely stationary, whereas during *searching* the dormouse body was still, but the head was exploring, or nosing, around its environment. *Grooming* was a self-groom of the paws or other body areas. As the Bushnell HD camera is triggered by simultaneous heat and movement detection, all recorded videos are during *active* behaviour.

Statistical Considerations

Kruskall-Wallis and follow-up Mann-Whitney *U* tests were performed on DV whisker variables (three substrate types), with Mann-Whitney *U* tests for the RC whisker variables (two substrate types). Relationships between locomotion speed and whisker kinematics were performed using one-tailed Pearson's correlation tests using bootstrapping (1000 iterations). The frequency of dormouse positions and behaviours from the camera trap footage was tested using chi-square. No significant differences were observed between individuals or sex.

Results

Dormice move their whiskers whilst locomoting along a flat floor

When exploring on a flat floor, dormice positioned their whiskers with a mean angular position (*RC set point*) of 127.22°. Compared to our previously published data (Mitchinson et al. 2011) this indicates that, on average, dormice push their whiskers further in front of the snout than either rats (100.63°) or mice (112.53°). Note, however, that the *locomotion speed* of dormice (13.82 cm/s on a flat floor) was also faster than that of both rats and mice in our earlier study. Dormice also moved their whiskers with broader back and forth sweeps (higher *RC amplitude*), and more *frequently* in the *RC* plane than rats, but less so than mice. See **Table 1** for a breakdown of all means and standard deviations, and **Video A** (Online Resource 1) for an example of whisking whilst locomoting along a flat floor.

Dormice alter their whisking strategy according to the substrate they are locomoting along, and the speed at which they travel

Dormice moved much more quickly around the climbing arena ($M = 56.99$ cm/s on a flat substrate, see **Fig. 4a**) than in the flat floor arena ($M = 13.82$ cm/s [$U = 6.00, p < .01$]), and adopted different whisker sensing strategies according to the orientation of the substrate and the task at hand. For instance, when reaching over a gap to a platform, dormice made much larger (higher *RC amplitude* [$U = 24.00, p < .05$]) and more frequent (higher *RC frequency* [$U = 33.00, p < .05$]) whisker sweeps than when exploring on the floor, as well as having greater asymmetry between the left and right whisker fields (higher *RC asymmetry* [$U = 26.00, p < .05$]), a strategy illustrated by the whisker traces in **Fig. 2** (left hand column). Whisking set-point was not significantly different between different substrates ($U = 39.00, p = .163$). Animals also showed a “look-ahead” whisking strategy during fast-paced locomotion (see **Fig. 3** and **Video B** (Online Resource 2), involving pushing the whiskers further in front of the snout with increasing locomotion speed ($r^2 = .274, p < .05$), matching our earlier findings in rats (Arkley et al., 2014).

As confirmed by investigating high-speed video data in the side-on view, dormice adjusted their whisking behaviour in the DV plane depending on context (**Fig. 4**). Specifically, animals adapt the set-point of their whiskers whilst locomoting along different substrates ($\chi^2(2) = 9.74, p < .01$), for example by positioning their whiskers more rostrally (towards the direction of travel) when locomoting along a flat floor as opposed to a sloped substrate ($U = 54.00, p < .05$) or exploring over a gap ($U = 6.00, p < .01$) (**Fig. 4b**), whereby the whiskers are directed more towards the ceiling. Animals also reduced the amplitude of their DV whisker movements when searching over a gap ($U = 12.00, p < .05$) (**Fig. 4c**), and moved more quickly on a flat substrate than on a sloped substrate ($U = 44.00, p < .01$) or over a gap ($U = 14.00, p < .05$) (**Fig. 4a**). There were no significant differences between DV whisking *frequency* when locomoting on different substrates or over a gap ($\chi^2(2) = 1.79, p = .408$) (**Fig. 4d**) (see **Video C**, Online Resource 2). Qualitatively, as shown in the video stills in **Fig. 4e-f** and observed in all video data, animals on flat and sloped substrates held their ventral-most whisker tips close to the ground at all times during forward locomotion, whilst there was much greater movement in the dorsal-most whiskers. As only the dorsal-most whiskers are tracked in our analyses we are therefore only able to partially describe the kinematics of whisker motion in the DV plane.

Gap crossing abilities and the effect of habitat gaps on dormouse behaviour

As shown in **Table 2**, dormice could successfully cross gaps of 21-28 cm (the maximum possible distance within the climbing arena). The average *whisker reach* was 6.31±1.21 cm (with one male dormouse having a whisker reach of 8.24 cm), and the crossing distances were far greater than the animals’ whisker reaches. There was no relationship between whisker reach and maximum gap size crossed ($r = -.54, p = .46$), for example, the male dormouse with the largest whisker reach made the smallest gap cross. See **Video D** (Online Resource 3) for an example.

Despite these large distances crossed, as the gap size increased, the number of times the dormice crossed decreased ($r = -.790, p < .05$). This can be seen in **Table 3**, where the values were normalised against the number of crossings without a gap. For instance, at gap sizes of 25 cm, dormice crossed 75% less often than when there was no gap. Increasing the gap size also had a significant effect on dormice location in the arena (χ^2 (18) = 320, $p < .001$) and on the behaviours they engaged in (χ^2 (36) = 663, $p < .001$). As can be seen in **Fig. 5a**, when gap size is ≥10 cm dormice spend more time on the ground of the arena and less time on the fruit platform, and also spend more time travelling (walking, climbing) than eating fruit when the gap size is ≥15 cm (**Fig. 5b**).

Discussion

This is the first study to quantify dormouse whisker movements using high-speed videography. Like many other rodents, dormice actuate their whiskers, moving them back and forth in large sweeps during exploration and locomotion. This study also confirms that dormouse whisking, like that of rats and mice, is actively controlled (Prescott et al. 2011), that is, they appear to purposively adapt the movement and position of their whiskers depending on task demands, for instance according to the substrate they are locomoting along, or whilst exploring over gaps between platforms. Dormice are distant relatives of the murid rodents in which whisking has been most extensively studied, the current study therefore lends weight to the view that active whisker sensing may be an ancestral trait of early rodents (Mitchinson et al. 2011; Grant et al. 2013).

Our data also show that dormice are able to cross large gaps between platforms (up to our maximum gap distance of 28 cm), but that larger habitat gaps impacted general dormouse behaviour by increasing travelling behaviours and time spent on the ground (as opposed to eating). In the remainder of this discussion, we consider the benefit of active whisker sensing for the arboreal habitat of the dormouse, and consider the impact of habitat gaps on the future of this protected species.

Whiskers guide complex locomotion

The amplitude and frequency of dormouse whisker movements fall between the values recorded in mice and rats, perhaps owing to their intermediate size. Whilst locomoting and exploring open arenas with flat floors dormice adopted a whisker position that was further forward of the snout than in rat or mouse (**Table 1**). However, as we have previously shown in rats (Arkley et al. 2014), dormice also modify whisker set-point according to running speed such that the faster the animals run the further in front of the snout they hold their whiskers. In rats we have argued that this behaviour reflects an increased emphasis on collision avoidance as animals move faster, and reflects an active sensing strategy of increasing “look-ahead” where there is greater risk of forward collision. This cross-species strategy may be particularly advantageous in an arboreal environment. Indeed, small nocturnal and arboreal mammals have been found to have longer whiskers with a more densely packed whisker field than those of ground-dwelling and burrowing mammals (Ahl, 1986; Pocock, 1914).

As with other rodents, the whisker movements of dormice includes components in the RC plane and in the DV plane relative to the head. Since we were unable to simultaneously film in both the overhead and side-on views we are not able to precisely decompose these two components of movement or say how they vary together, but evidence from rats suggest that they should be closely coupled (Knutsen and Ahissar 2008). Interestingly, whisker set point in the DV plane varied according to whether dormice were locomoting along a flat or sloped substrate, or exploring a gap **Fig. 4b**. Specifically, the dorsal-most whiskers were positioned more towards the ceiling during gap exploration, and directed more towards the direction of travel on a flat floor and to a lesser extent on a sloped substrate.

When travelling along flat substrates it was observed that, although the dorsal-most whiskers periodically palpated near the floor during locomotion (**Fig. 4e**), the ventral-most whiskers almost always contacted the ground or pole (**Fig. 4b and e**, **Fig. 6a,** and **Video E,** Online Resource 5). For this reason, these whiskers were unable to be tracked, but it suggests that dormice may be strategically and continuously sampling the floor in order to guide locomotion and the placement of safe footfalls, whilst simultaneously monitoring the space above the head. As this DV shift of the dorsal-most whiskers, noted above, was maintained throughout the whisk cycle (**Fig. 4g**), it seems likely that this is due to the action of the *vertical-moving muscles*, rather than the protracting intrinsic muscles. Recording the whisker movements of other rodents exploring in 3D environments may be worthwhile to further explore variability in DV whisker movements. Dormice also significantly increase RC whisk amplitude during gap exploration sweeping the whiskers back and forth in larger sweeps (**Table 1, Fig. 2**), indicating an active modulation of their search strategy when looking for substrates that will support locomotion, a pattern that we have also observed in other rodents.

There have been relatively few previous investigations of gap-crossing in dormice. Kahmann and Ostermann (1951) observed dormice (*Glis glis*) jumping long distances (40cm) to a food platform, however, a replication by Airapet'yants, reported in Thomas et al. (2004), found that dormice would only cross to a food platform that they were able to reach with their whiskers. Neither study included filming of the whiskers, so the data is inconclusive in terms of understanding the role whisker touch sensing in dormouse gap-crossing. In our study dormice crossed gaps more often if they could physically reach the landing platform by palpating across the gap with their whiskers immediately prior to crossing (**Fig. 6a**). In these cases whisker palpations on the opposite side of the gap always preceded any forepaw contact. However, we also observed that dormice are capable of making much larger jumps. In a small number of cases (only two high-speed video clips captured, but more using the camera trap) we observed dormice jumping from poles and branches, and across gaps where the whiskers were too short to be able to contact the platform edge (or floor) prior to take-off. An example of a large jump can be seen in **Fig. 6b**, which clearly shows that the animal was unable to reach the landing surface (the floor) with their whiskers prior to jumping. Under these circumstances the whiskers were pushed out in front of the animal and back-and-forth whisker movement was greatly reduced (compare **Fig. 6b** to **Fig. 6a**). This would indicate that, when jumping without prior tactile information about the landing site, dormice push their whiskers further forward in order to gain some additional time in which to prepare for a safe landing. Such a "look-ahead" for jumping would match the similar strategy described above (and in Arkley et al. 2014) for collision-detection when locomoting at speed. Although the whiskers are important in dormouse gap crossing, vision is certainly also significant in guiding orientation around the canopy (Grzimek et al. 2004), especially for larger gaps. The ability to cross gaps will therefore be significantly impacted by light availability.

Interestingly, there were differences between individual dormice in the maximum distances of the gaps crossed, irrespective of their whisker reach (**Table 2**). This might suggest that the ability to jump over large gaps in dark or dimly lit environments is also affected by the "personality" of the animal. Dispersal in other small mammals has been found to be linked to boldness, sociability and aggression (Cote et al. 2010; Raynaud and Schradin 2014), and may present a useful focus for future work on dormice biology and ecology.

Impact of gaps in the canopy

Even though dormice may be capable of crossing up to 40 cm by jumping (Thomas et al. 2004), and 50-200 m by walking on open ground (Buchner 2008; Mortelliti et al. 2013), we show here that having even very small gaps in the canopy can have an impact on dormouse behaviour. We propose that habitats should be very closely connected in order for dormice to move around frequently and with ease using whisker touch sensing. As echoed by Bright (1998) and Mortelliti et al. (2011), hedgerows are the ideal candidate for connecting habitat patches, and will encourage movement of the UK's declining dormouse populations towards suitable new homes and food sources.

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Figures

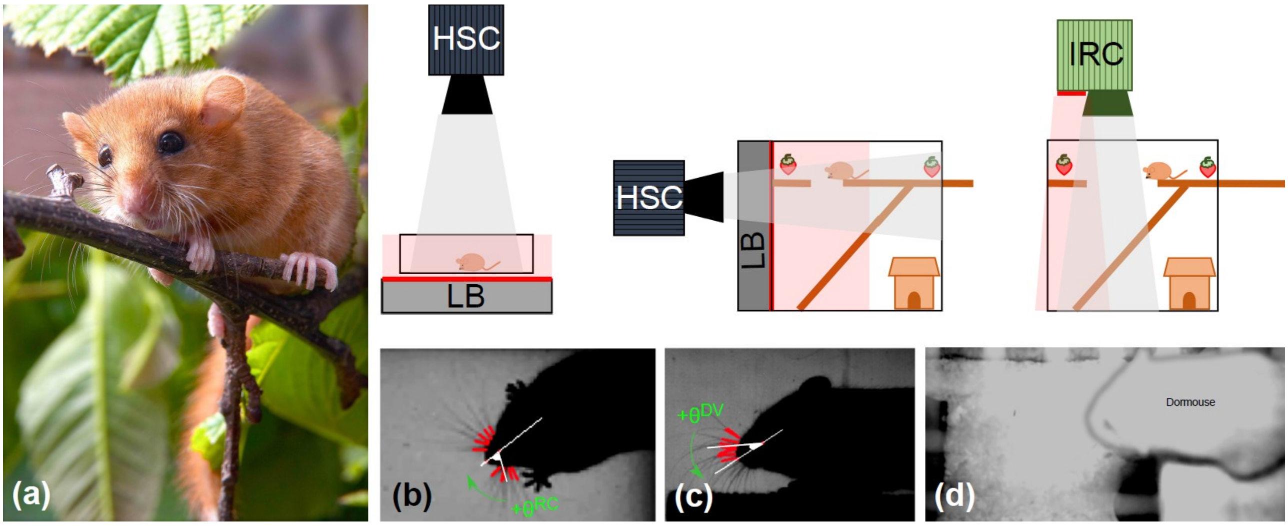

Fig. 1

Experimental set-ups and example video data recorded with whisker tracking overlaid and schematic showing extracted angular position of the whiskers relative to head for both top-down and side-on views (a) Image of a Hazel dormouse (b) Flat floor surface in open arena filmed with high-speed camera from over-head (top-down) (c) climbing arena filmed predominantly side-on, however, some gap exploration behaviour was recorded top-down (d) climbing arena filmed top-down with infrared camera trap. Example video stills recorded from each set-up can be seen below the illustrations, along with overlaid tracked snout midline (white) and whiskers (red). HSC = high-speed camera; LB = infrared lightbox; IRC = infrared camera trap

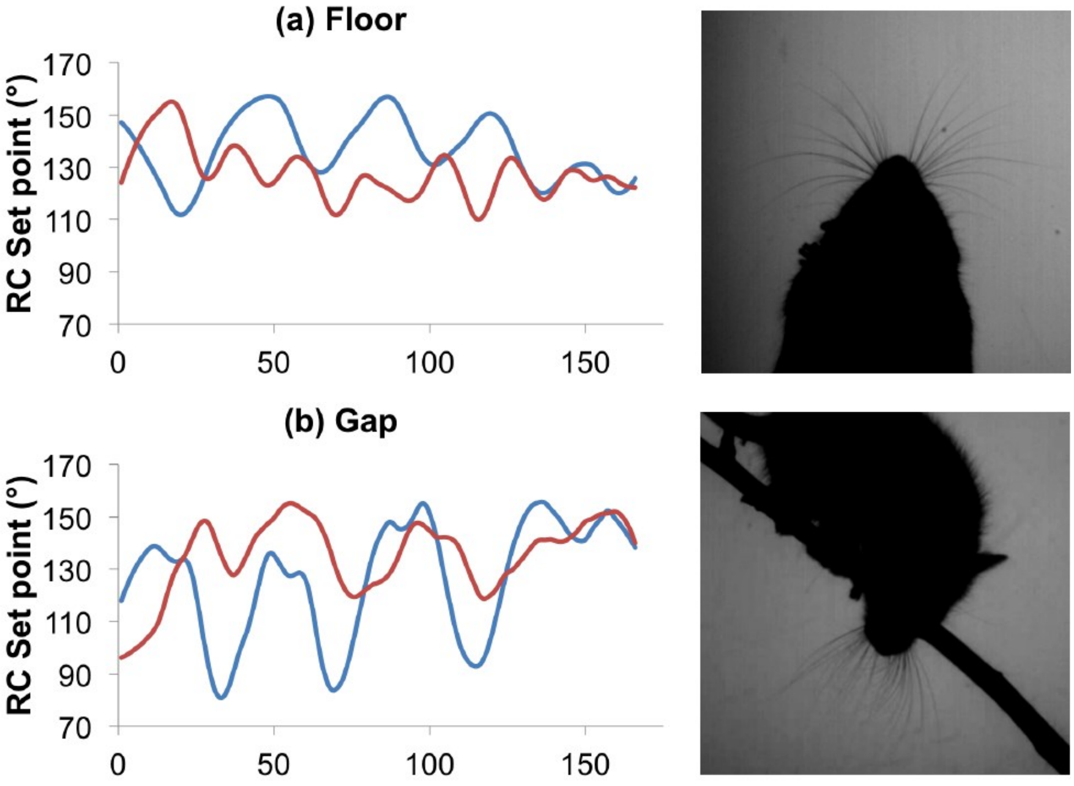

Fig. 2

Example RC whisker traces (left) and video stills (right) from a dormouse (a) locomoting on a flat substrate and (b) exploring over a gap. As shown in the whisker trace examples (RC whisker set-point of left [blue] and right [red] whisker fields), dormice move their whiskers at higher amplitudes whilst exploring gaps than on a flat floor

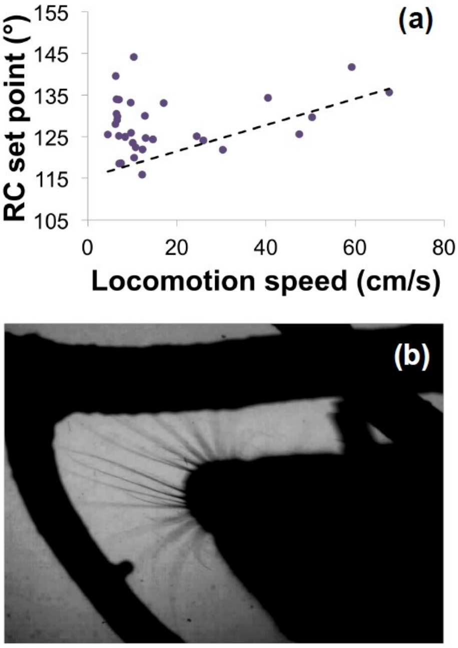

Fig. 3

Evidence for a “look-ahead” whisking strategy. (a) Scatterplot showing a significant positive relationship between locomotion speed and RC set-point ($r^2 = .274$, $p < .05$), such that dormice push their whiskers further in front of their snout as they run at a faster pace. (b) High-speed video still of a dormouse in our flat floor arena displaying a strong look-ahead whisking strategy whilst locomoting at speed

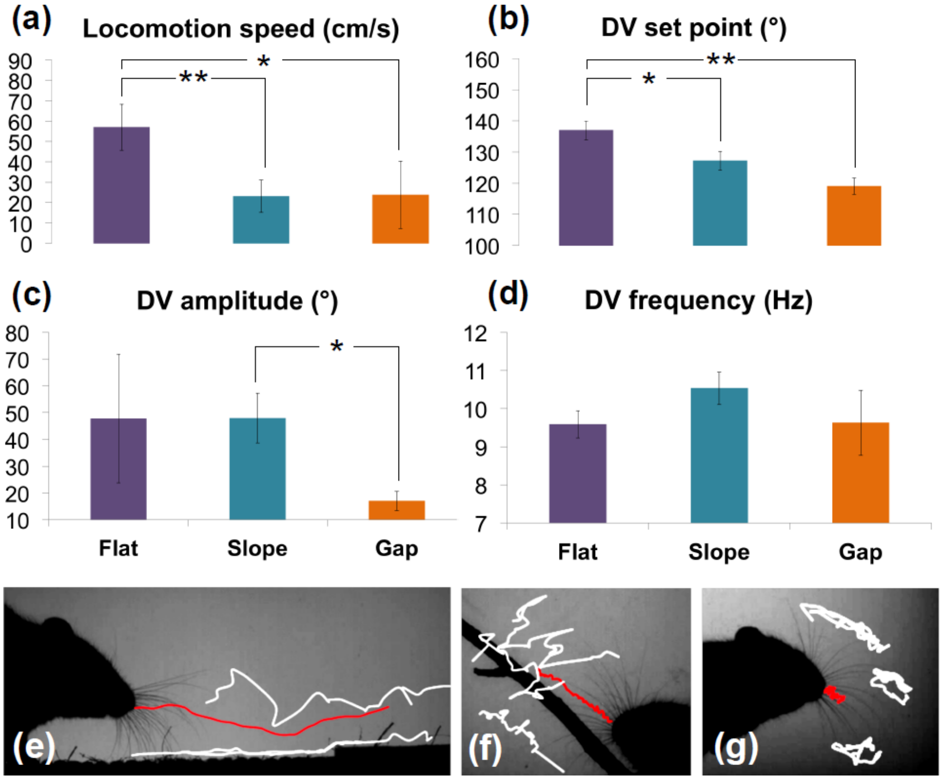

Fig. 4

Effect of climbing substrate on locomotion and whisking variables. (a)-(d): Histograms showing whisking variables: (a) locomotion speed, (b) DV whisker set point, (c) DV whisk amplitude, (d) DV whisk frequency, from side-on video footage of dormice in climbing arenas on *flat substrates*, *sloped substrates*, and *exploring over gaps*. Stars denote significance (* $p < .05$, ** $p < .01$). (e)-(g): Example video stills of dormice (e) locomoting on a flat substrate, (f) locomoting on a sloped substrate, and (g) exploring over a gap. Manually tracked whisker tips (most-ventral, most-dorsal, midline) are overlaid in white, and the snout tip in red

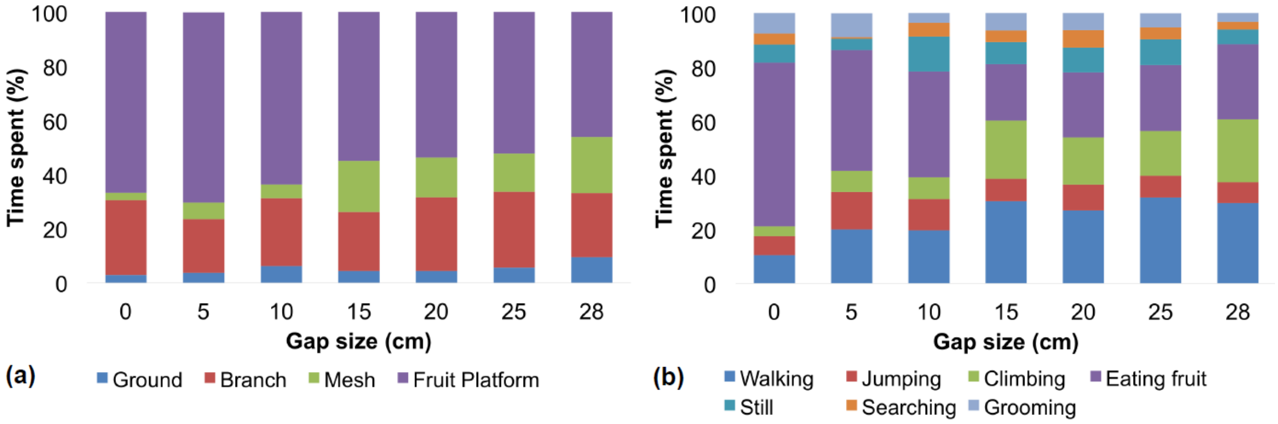

Fig. 5

Proportion of active time spent in (a) different locations and (b) engaging in different behaviours within the climbing arena as gap size between fruit platforms increases

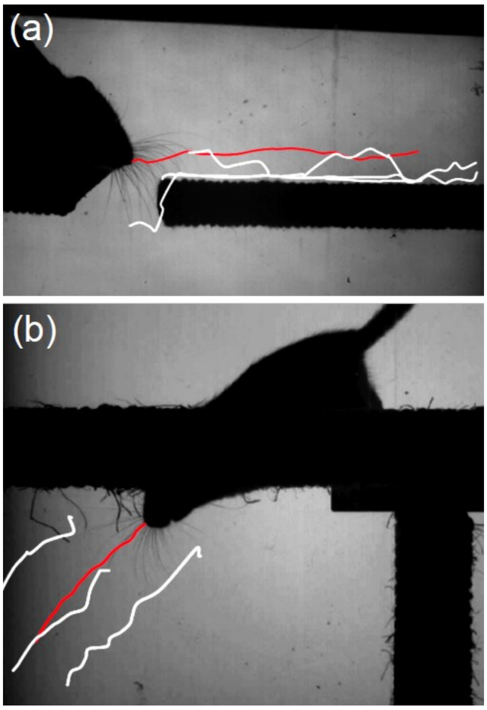

Fig. 6

Example high-speed video stills of dormice (a) engaging in gap crossing and locomoting along a flat substrate and (b) making a large jump to the floor that is much greater than whisker reach (see also corresponding **Video D**, Online Resource 3). Manual tracking of the snout tip is overlaid in red, as well as three whisker tips (ventral-most, midline, and dorsal-most) in white