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Whisker touch sensing guides locomotion in small, quadrupedal mammals

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Abstract

All small mammals have prominent facial whiskers that they employ as tactile sensors to guide navigation and foraging in complex habitats. Nocturnal, arboreal mammals tend to have the longest and most densely-packed whiskers, and semi-aquatic mammals have the most sensitive. Here we present evidence to indicate that many small mammals use their whiskers to tactually guide safe foot positioning. Specifically, in eleven, small, non-flying mammal species we demonstrate that forepaw placement always falls within the ground contact zone of the whisker field, and that forepaw width is always smaller than whisker span. We also demonstrate commonalities of whisker scanning movements (whisking) and elements of active control, associated with increasing contact with objects of interest, across multiple small mammal species that have previously only been shown in common laboratory animals. Overall, we propose that guiding locomotion, alongside environment exploration, is a common function of whisker touch sensing in small, quadrupedal mammals.

Keywords: whisking, forepaw, rodents, arboreal, nocturnal, semi-aquatic

Background

All mammals have facial whiskers, with the exception of great apes and humans. Whiskers are sensitive tactile hairs that guide behaviours, such as navigation, locomotion, exploration, hunting and social touch (Prescott et al. 2011; Grant & Arkley 2016). The overall layout of the whiskers and their specialist facial musculature is conserved from marsupials (Grant et al. 2013), to rodents (Haidarliu et al. 2010; 2017) to nocturnal primates (Muchlinski et al. 2008). Small, social, arboreal and nocturnal mammals tend to have the longest and densest whiskers (Muchlinski et al. 2010) and aquatic mammals the most sensitive whiskers (Dehnhardt et al. 1999). Therefore, mammals that forage and navigate in dark, complex habitats are likely to use their whiskers more, and are also often able to actively position and move them (Muchlinski et al. 2013; 2018). Indeed, Brown rats (*Rattus norvegicus*), Golden hamsters (*Mesocricetus auratus*), House mice (*Mus musculus*) and many other small mammals actively move their whiskers in a bilateral, cyclic motion, called whisking, which is one of the fastest movements that mammals can make, occurring at speeds of up to 25 Hz in mice (Mitchinson et al. 2011).

Whisker positioning and movement has strong associations with locomotion. While adult rats will whisk bilaterally and symmetrically during forward locomotion, at higher speeds (> 150 cm/s) they will reduce whisker amplitudes and position their whiskers more forward, in order to focus the whiskers in front of their snout, in a behaviour termed 'look ahead' (Arkley et al. 2014). The same strategy can be seen when Hazel dormice (*Muscardinus avellanarius*) and House mice (*Mus musculus*) make large jumps and stretch across gaps (Jenkinson and Glickstein 2000; Arkley et al. 2017), where the whiskers are focussed forward to act as collision detectors and protect the delicate area in front of the snout (Arkley et al. 2014).

Stretching the whiskers out in front of the face also reduces the time to collision (Arkley et al. 2014), which increases the time in which to prepare for a safe landing following a jump (Arkley et al. 2017). During climbing or walking on a flat floor, whiskers are often thought to scan ahead and guide safe foot positioning (Arkley et al. 2014; 2017). This has been observed in Brown rats (*Rattus norvegicus,* Arkley et al. 2014), Hazel dormice (*Muscardinus avellanarius*, Arkley et al. 2017) Long eared jerboas (*Euchoreutes naso*) and Northern three-toed jerboas (*Dipus sagitta)* (Sokolov and Kulikov 1987). Indeed, Sokolov and Kulikov (1987), found that nocturnal, terrestrial Jerboas used their whisker tips to scan along the floor directly where their paws fell, suggesting that the whiskers provided information about where the animal would subsequently place its feet. However, these observations have yet to be fully quantified.

The degree to which the whiskers are moved and controlled varies greatly from species to species. Brown rats (*Rattus norvegicus*) and House mice (*Mus musculus*) whisk, and can control their whiskers in robust and repeatable ways during locomotion and object exploration, by altering the timing, spacing and positioning of their whiskers (Arkley et al. 2014; Berg & Kleinfeld 2003; Grant et al. 2009; 2013; Mitchinson et al. 2007; 2011). The effect of these active whisker control strategies may be to increase the number of controlled whisker contacts with surfaces of interest. For instance, by asymmetrically modulating the amplitude of whisker movements on the two sides of the snout when a surface is encountered unilaterally, termed contact-induced asymmetry (CIA), animals can increase the number of contacts whilst avoiding excessive whisker bending (Mitchinson et al., 2007; 2011). Some elements of whisker control are absent in the whisking, nocturnal, arboreal grey short-tailed opossum, *Monodelphis domestica* (Grant et al. 2013; Mitchinson et al. 2011), which is considered to be useful model of early mammals. Specifically, although *M. domestica* shows whisking and CIA it is unable to alter whisker spread, another strategy thought to increase the number of whisker contacts (Grant et al., 2009). Diurnal, terrestrial Domestic Guinea pigs (*Cavia porcellus*) do not whisk and can only make few, asymmetric twitches of their whiskers, rather than the bilateral, cyclic movements associated with whisking (Grant et al. 2017). However, the striking presence of whiskers in all small mammals, even in diurnal terrestrial mammals, as well as the conservation of their arrangement and facial whisker musculature, suggests that they might be still functional in all small mammals (Grant et al. 2017). We propose in this study that in addition to environment exploration, guiding locomotion might be a common function of whiskers in small mammals.

This study will, for the first time, compare whisker movements and control during locomotion in a range of diurnal, nocturnal, crepuscular and cathemeral small mammals, with varying substrate preferences (arboreal, terrestrial and semi-aquatic) focusing on the role of facial whiskers in guiding locomotion and foot positioning.

Methods

Animals

Eleven species of small mammals were considered in this study (59 individuals, Supplementary Material, Supplement 1). This included the nocturnal, arboreal Hazel dormouse (*Muscardinus avellanarius*), Etruscan shrew (*Suncus etruscus*), Woodmouse (*Apodemus sylvaticus*) and Yellow-necked mouse (*Apodemus flavicollis*); the crepuscular, arboreal Harvest mouse (*Mycromys minutus*); the cathemeral, arboreal Brown rat (*Rattus norvegicus*), cathemeral, semi-aquatic Water shrew (*Neomys fodiens*) and cathemeral, terrestrial Pygmy shrew (*Sorex minutus*); the diurnal semi-aquatic Water vole (*Arvicola* *amphibious*), the diurnal, terrestrial Bank vole (*Myodes glareolus*) and the Domestic Guinea pig (*Cavia porcellus*). The Etruscan shrews (*Suncus etruscus*) were wild-caught and maintained at the Bernstein Center for Computational Neuroscience, Berlin, Germany. Domestic Guinea pigs (*Cavia porcellus*) were domestic and maintained at Heeley City Farm, Sheffield, UK. The rest of the animals were tested at the Wildwood Trust, Kent, UK, and were either part of breeding programs, rehabilitation programs or for visitor displays. All animals were adult, with males and females represented where possible. Whisker movements were assumed to be sexually monomorphic.

Whisker movements on a flat floor

All eleven species were used in this section of the study. Animals were placed in to a Perspex arena (Figure 1a) using cardboard tubes to prevent excessive handling. They were filmed directly from above or below using a high-speed, high-resolution video camera at 500 fps (either Phantom Miro ex2 or Photron Fastcam) (Figure 1a, left; Supplementary Material, Supplement 1). Animals that were filmed from below, were imaged through the pedobarograph floor (Figure 1a). An infrared light-box illuminated the arena, allowing video clips to be collected in semi-darkness. In some instances, a Perspex block was introduced to the arena to promote object exploration. Multiple video clips were collected opportunistically (by manual trigger) when each animal was locomoting around or exploring the block, and range from 0.6-1.6 seconds in length. Recording stopped when the camera memory was full, the animal stopped exploring, or became stressed. In total, 780 clips were collected from 59 individuals. The number of clips and the number of individuals filmed can be seen in Supplementary Material, Supplement 1. The activity pattern (nocturnal, crepuscular, cathemeral, diurnal and substrate preference (arboreal, terrestrial, semi-aquatic) were also recorded for each species in Supplementary Material, Supplement 1. These groupings can often be difficult to strictly define. Indeed, here we refer to cathemeral animals as those species which are flexible enough to be active at many time of the day and not strictly just at night time; including *Rattus norvegicus*, *Sorex minutus,* and *Neomys fodiens.*

From the 780 clips collected, those suitable for whisker tracking were selected resulting in two to eight clips per individual and a total of 207 clips (Supplementary Material, Supplement 1). These clips included episodes where the animal was locomoting and not contacting a vertical surface with its whiskers, such as the block or arena wall. In addition, the snout and both whisker arrays had to be clearly visible throughout the clip selection, with minimal head pitch or roll. The whiskers and head were tracked semi-automatically using the BIOTACT Whisker Tracking Tool (Perkon et al. 2011) (Figure 1b), the mean whisker angular positions (relative to the head) was derived for each side of the head. To estimate *amplitude* the mean value was removed from the mean whisker angular positions, and the root mean square value was computed to give the root-mean-square (RMS) whisking amplitude. As the mean whisker angular positions were approximately sinusoidal, the "peak-to-peak whisking amplitude" was estimated by multiplying the RMS whisking amplitude by $2\sqrt{2}$ (Chatfield 2003). This estimate of amplitude is reasonably robust to departures from a purely sinusoidal pattern (Grant et al. 2014). The *whisking frequency* was estimated from a Fourier transform of the mean whisker angular position data. The *whisker offset*, was calculated as the mean whisker angular positions. Mean angular *retraction* and *protraction speeds* were also calculated as the average velocity of all the backward (negative) and forward (positive) whisker movements, respectively. Mean amplitude, frequency, speeds and offset were calculated for left and right whiskers and then averaged to give a per clip measure. Locomotion speed (m/sec) was also approximated from the position of the nose tip.

Refer to the methods section in Grant et al. (2014) for more information on the whisker variables.

Each of the 780 clips were also reviewed to see if certain whisking behaviours were present or absent for a particular species. These categorical whisking behaviours were *whisking, spread reduction, contact-induced asymmetry (CIA)* and they were reviewed using scales developed in Grant et al. (2012). Whisking was scored during clips where the animal was locomoting forward, either as retractions and protractions present, or only retractions present. Spread reduction and CIA were scored in clips where the animal's whiskers were contacting the perspex block or arena walls. Spread reduction was scored as simply being present or absent; CIA was scored as present, with both an increase in contralateral whisker angles and decrease in ipsilateral whisker angles, or only the decrease in ipsilateral angles present. *Look ahead* behaviour was also reviewed, which was the presence of a positive correlation (Spearman's Rank) between locomotion speed and whisker offset.

Whisker movements on an inclined plane

Seven species were selected for inclusion in this section of the study, chosen for their larger sample sizes. These included Guinea pig (*Cavia porcellus*), Water shrew (*Neomys fodiens*), Water vole (*Arvicola amphibious*), Harvest mouse (*Miycromys minutus*), Brown rat (*Rattus norvegicus*), Woodmouse (*Apodemus sylvaticus*) and Hazel dormouse (*Muscardinus avellanarius*). Animals were filmed from below, through the pedobarograph (Figure 1a), in the arena with a flat floor, and then two to four animals of each species were filmed again the next day in the same arena inclined at an angle of 10 degrees (Figure 1a, right). Measures of whisking amplitude, frequency, speed, offset and locomotion speed were extracted in the same way as for the flat floor section of the study to enable a direct comparison. Whisker span was measured from the footage, as the smallest whisker width in the video, when the whiskers were at maximum protraction (Figure 1b). The forepaw width was also measured as the width between the two forepaws (Figure 1c). These relative values are presented in the text, where the size of the animal was controlled for by approximating the Geometric mean of the head from head width and length (GM = square root (head width x length)) measurements from the video (Supplementary Material, Supplement 2). It was not possible to identify morphological features in the footage to guide these measurements, therefore the maximum head width was identified, with the length then measured from this point to the nose tip. Maximum shoulder and hip width was also measured for all species, from the videos and presented as a ratio in Supplementary Material, Supplement 2, to get an idea of general body shape; a value over one indicates that the hip width is larger than the shoulder width.

Foot positions on a flat and inclined floor

For the seven species filmed on both the flat and inclined plane, it was possible to identify foot contacts using the pedobarograph, which is a glass floor, illuminated with a strip of red LEDs to highlight foot contacts (Figure 1c). Foot positions and nose positions of each species were tracked manually in three example clips when the animal locomoted forward across the floor using the program Tracker (Tracker 4.80, Brown and Wolfgang 2013, http://www.cabrillo.edu). The minimum distance of foot placements to the nose tip was calculated, as well as the time it took from the nose point to move from the minimum distance point and foot placement to arrive. The gait cycle was also calculated (in Hz) from the time a front paw contacted the ground to when the same paw contacted the ground again.

Statistical Considerations

Whisking results for all eleven species are presented in Table 1 and Supplementary Material, Supplement 4 as mean values ± standard deviations. Whisking variables and locomotion speed were compared on flat and inclined floors using a MANOVA, individual multivariate ANOVAs were conducted for each of the seven species that were tested on the flat and inclined planes. Locomotion speed was correlated against amplitude, offset and frequency for the nocturnal, crepuscular, cathemeral, and diurnal species groupings, using a Spearman's Rank Correlation. Whisker span, foot span and offset were also correlated for the nocturnal, crepuscular, cathemeral, diurnal species groupings, using a Spearman's Rank Correlation.

Results

Whisker movements in small mammals

All eleven of the small mammals can control movements of their whiskers to some extent. Rhythmic whisking was observed in all of the species tested, apart from *Cavia porcellus* (Table 1), which made isolated unilateral whisker twitches instead. This can be clearly seen in the example whisker traces in Figure 2a, vii, where the left whiskers of *Cavia porcellus* (in blue) made low amplitude, rhythmic movements, but the right whiskers (in red) were just slowly moving forward, with no rhythmic movements. On review of the video footage, whisking in *Neomys fodiens* looked to only consist of retraction movements, but all other species engaged in rhythmic, bilateral, forward and backward whisker sweeps (Table 1). Examples of these whisker sweeps can be seen in Figure 2a, and varied between the species in terms of amplitude, frequency, offset asymmetry and speeds (Table 1). For example, *Rattus norvegicus* and *Apodemus flavicollis* had large amplitude whisks (Figure 2a, iv and ii , respectively), while *Muscardinus avellanarius* had the most forward facing whiskers, with the largest offset values (Table 1, Figure 2a, i).

Table 1 Whisker measurement results for each species on a flat floor, shown as mean ± s.d. Grey boxes in the species column show the animals that were also tested on the inclined floor; grey boxes in the whisker variable columns, correspond to variables that significantly altered when the same animals were filmed on an inclined floor.

Species	**Loco Speed m/sec**	**Freq Hz**	**Off deg**	**Amp deg**	**Asym deg**	**Pro Speed deg/ms**	**Re Speed deg/ms**	**Whisk**	**Spread**	**CIA**	**Look ahead**
European Dormouse *(Muscardinus avellanarius)*	0.53± 0.48	9.60± 3.88	126.19± 8.21	37.83± 16.30	18.25± 7.41	1.57± 0.28	0.24± 0.16	Present	Present	Present	Present
Etruscan Shrew *(Suncus etruscus)*	0.26± 0.10	10.13± 3.03	87.56± 11.49	29.56± 4.41	16.45± 8.49	1.41± 0.09	0.20± 0.08	Present	Absent	Ips. Only	Present
Woodmouse *(Apodemus sylvaticus)*	0.34± 0.26	16.08± 7.05	117.28± 10.09	36.57± 7.26	11.95± 3.78	1.69± 0.31	0.43± 0.23	Present	Present	Present	Present
Yellow-necked mouse *(Apodemus flavicollis)*	0.40± 0.20	13.67± 2.14	101.68± 12.72	46.06± 11.27	19.00± 10.26	1.57± 0.10	0.53± 0.19	Present	Present	Present	Present
Harvest Mouse *(Micromys minutus)*	0.28± 0.07	12.03± 4.49	99.76± 6.77	45.67± 11.86	17.82± 3.65	1.87± 0.41	0.51± 0.21	Present	Present	Present	Absent
Brown Rat *(Rattus norvegicus)*	0.27± 0.15	8.80± 0.76	107.23± 8.90	44.22± 7.96	17.95± 3.00	1.34± 0.10^{l}	0.15± 0.05	Present	Present	Present	Absent
Water Shrew *(Neomys fodiens)*	0.39± 0.19	8.08± 4.81	104.45± 6.80	39.22± 13.39	16.04± 4.71	1.74± 0.41	0.42± 0.37	Ret. only	Absent	Present	Absent
Pygmy Shrew *(Sorex minutus)*	0.64± 0.22	14.80± 4.46	91.78± 10.30	39.25± 8.51	15.42± 6.14	1.84± 0.24	0.54± 0.20	Present	Present	Ips. Only	Absent
Water Vole *(Arvicola amphibious)*	0.15± 0.12	8.27± 3.47	117.51± 7.49	40.97± 23.97	26.56± 9.47	2.03± 2.44	0.20± 0.22	Present	Present	Ips. Only	Absent
Bank Vole *(Myodes glareolus)*	0.83± 0.61	13.75± 3.18	126.08± 14.14	27.84± 10.52	9.65± 3.12	1.37± 0.18	0.27± 0.23	Present	Present	Present	Absent
Domestic Guinea pig *(Cavia porcellus***)**	0.26± -0.07	n.a.	104.22± 7.11	36.68± 23.51	30.75± 13.69	n.a.	n.a.	Absent	Absent	Absent	Absent

As well as whisking, other elements of whisker control also varied between the species. Spread reduction was absent in *Suncus etruscus* and *Neomys fodiens*, and contact-induced asymmetry was limited to only a decrease in ipsilateral whisker angles, without any increases in contralateral angles, in *Suncus etruscus, Sorex minutus* and *Arvicola amphibious*. *Cavia porcellus* did not engage in spread reduction or contact-induced asymmetry. When the animals were placed on an inclined floor, aspects of whisker position and movement were significantly altered in all of the tested species, apart from *Cavia porcellus* (Table 1, Supplementary Material, Supplement 4). While locomotion speed was not significantly affected in any of the species (F(1,106)=0.748, p=0.389), generally, whisker speeds were reduced as well as whisker amplitudes. Supplementary Material, Supplement 4 shows three example whisker traces from *Micromys minutus, Arvicola amphibious* and *Neomy fodiens*, who all showed significant reductions in amplitude on the inclined floor compared to the flat floor.

The lengths of the whiskers varied between species, even when controlling for body size. Figure 2c shows a diagram taken from tracing around the head and whiskers, and exact whisker lengths (controlled for by body size) can be seen in Supplementary Material, Supplement 2. *Rattus norvegicus* had the longest whiskers (relative length: 2.82±0.26, Figure 2c), followed by *Apodemus sylvaticus* (relative length: 2.24±0.36, Figure 2c) and *Muscardinus avellanarius* (relative length: 2.15±0.26, Figure 2c). *Micromys minutus* and *Neomy fodiens* had very similar whisker lengths (relative length: 1.69±0.23 and 1.68±0.21, respectively, Figure 2c), followed by *Arvicola_amphibious* (relative length: 1.61±0.11), and *Cavia porcellus* having the smallest whiskers (relative length: 0.88±0.15).

Whiskers and locomotion in small mammals

Despite variations in the length of their whiskers and the animals' abilities to move and control them, the forepaw placements of all the species tested always fell within an area that the whiskers had previously scanned. Indeed, in all the species tested, the forepaw placements fell 4-25 mm of where the nose tip had previously been. Analysis of the timings indicate that in small mammals the nose tip, and whisker field, scan an area 47-367 ms ahead of forepaw placements. There was more variation in rear paw placement, with the majority of rear paw placements falling 7-62 mm from a previous nose tip position, with a delay of 203-674 ms behind the nose tip scan. Some rear paw placements occurred outside the whisker field in *Muscardinus avellanarius, Rattus norvegicus, Arvicola amphibious, Cavia porcellus* and *Neomys fodiens* (Figure 2c). Figure 2b shows the distance of the fore (in blue) and hind (in red) paw placements from a previous nose placement. Forepaw placements fell closer to a previous nose tip location than hindpaw placements in all species tested. Figure 2c diagrammatically shows this, with mean paw positions (in bold colour) and standard deviations (in lighter shading) approximated on the traced whisker field for each species.

The animals travelled at varying speeds with their gait cycles varying from 1.76 Hz in rat, to 5Hz in guinea pig (Supplementary Material, Supplement 2); the gait cycle was not associated with species' whisking frequency (Spearman's Rank Correlation: r=0.143, df=6, p=0.787), such that species that moved quicker did not necessarily move their whiskers quicker.

There was no significant difference between footfall placement positions (Wilcoxon Signed Rank: W(12)=29, p=0.4328) or timings (W(12)=22, p=0.1823) with respect to previous nose tip positions, when comparing locomotion on a flat or inclined plane for any of the species tested. On an inclined floor, the same pattern was observed that forepaw placements fell closer to previous nose tip positons (6-34 mm) than hind paws (10-51 mm), with the nose position being 38-213 ms ahead of forepaw placements, compared to 119-382 ms ahead of hind paw placements. As there was no difference between paw placements on a flat and inclined plane, the data was combined in Figure 3a and b to explore the relationship between whisker span and forepaw width. In all species, forepaw width was always smaller than whisker span, indicating that forepaw placements fell within the whisker field (Figure 3a). Forepaw width and whisker span was also significantly correlated, with larger whisker spans being associated with larger foot widths in all the species tested, including nocturnal, crepuscular, cathemeral and diurnal individuals (Figure 3a, Supplementary Material, Supplement 3, all p-values <0.05). As whisker position impacts whisker span, with higher offset values being associated with smaller, more focussed whisker spans (Figure 3d) (Arkley et al. 2014), whisker offset was plotted against whisker span (Figure 2b). Whisker span was not correlated to mean whisker offset values (Figure 3a, Supplementary Material, Supplement 3, all p-values >0.05), although the nocturnal species showed the general trend that higher offset values were associated with smaller whisker spans (solid trendline in Figure 2b), especially in *Apodemus sylvaticus* and *Muscardinus avellanarius* (Figure 3b).

Whisker control varies in small mammals

While whisker offset was not correlated to forepaw width in any species (Supplementary Material, Supplement 3, all p-values >0.05), it was correlated to locomotion speed in all of the nocturnal species *Muscardinus avellanarius, Suncus etruscus, Apodemus sylvaticus* and *Apodemus flavicollis* (Figure 3c, Supplementary Material, Supplement 3, all p-values >0.05). Specifically, at higher locomotion speeds, the nocturnal species protracted their whiskers further forward, with higher offset values, which can be seen by comparing the example screenshots in the nocturnal *Muscardinus avellanarius* (Figure 3d) to the crepuscular *Micromys minutus* (Figure 3e) and the diurnal *Arvicola amphibious* (Figure 3f).

Discussion

Our results revealed that all the small mammals in this study could move their whiskers somewhat, although the degree of movement and control varied between species. All the species placed their forepaws on the floor, where their whiskers had previously scanned. This suggests that whiskers are likely to be functional and important in many small mammals, especially for guiding quadrupedal locomotion.

Whisker studies are often associated with nocturnal, or cathemeral, arboreal mammals, and this study is the first to consider whisker movement and control in a range of species. Indeed, this is the only study to have described whisker movements in *Apodemus sylvaticus, Apodemus flavicollis, Mycromys minutus, Neomys fodiens, Sorex minutus, Arvicola amphibious, Myodes glareolus* and to have quantitatively confirmed the presence of whisking in a large number of small mammals.

Whisker position is associated with locomotion

We found that all the species tested placed their forepaws in to an area that the whiskers had previously passed through. This has been suggested to occur in *Rattus norvegicus* (Arkley et al. 2014), *Muscardinus avellanarius* (Arkley et al. 2017), *Euchoreutes naso* and *Dipus sagitta* (Sokolov and Kulikov 1987), however, it was not fully quantified until now. In our species, all forepaw placements occurred within 4-25 mm of where the nose tip had previously been 47-367 ms before. We also found that forepaw widths were always smaller than the whisker span in the species we have tested, and that they were also correlated. This correlation suggests that if an animal increases the span of their whiskers, by spreading them out and reducing offset values, then the forepaw placements were also more spread out.

In our data, whisker scanning sometimes occurred one entire gait cycle ahead of the foot placement, but was much more likely to take place while the foot is off the floor, just prior to its placement on the ground. The most extreme example can be seen in *Micromys minutus*, where the gait cycle takes around 235 ms to complete (4.26 Hz), but the nose scanned only 47 ms ahead of the foot placement (Supplementary Material, Supplement 2). In rat (*Rattus norvegicus*), it can take 88-224 ms to make an action from a whisker contact, including discriminating textures or jumping on to a platform (von Heimendahl 2007; Diamond et al. 2008). These studies looked at discretely triggered actions, however, modulation of ongoing action may take place at multiple levels of the neuraxis from the brainstem through to cortex, at even shorter latencies. For instance, the latencies for whisker responses in rat somatosensory and in the midbrain superior colliculus can be as little as 5ms (Zhu and Connors 1999; Cohen et al. 2008), allowing whisker sensory processing to influence motor outputs well within the duration of typical gait cycle. Since whisking frequency can be more than twice as fast as stride frequency, whisker contacts over multiple cycles can be useful in guiding foot placements. In the laboratory house mouse (*Mus musculus*), aspects of whisking frequency have been found to be correlated to the gait cycle (Sofroniew et al. 2014). We did not observe any association between gait cycle and whisker frequency here, so species that moved faster did not necessarily whisk quicker.

However, other aspects of whisker positioning were controlled during locomotion. Whilst whisking and locomotion was generally similar on flat and inclined surfaces, all of the species, apart from *Cavia porcellus*, altered some aspects of whisker positioning or speed during locomotion on an inclined slope, compared to a flat floor. Moreover, at higher locomotion speeds *Rattus norvegicus* and *Mus musculus* have been found to reduce whisking and protract their whisker forward, in a process called 'look ahead', which is thought to focus the whiskers in front of the snout and prevent collisions with this sensitive area (Arkley et al. 2014; Sofroniew et al. 2014). This behaviour was observed in our data only in the truly nocturnal species, irrespective of substrate preference, including *Muscardinus avellanarius*, *Suncus etruscus, Apodemus flavicollis* and *Apodemus sylvaticus*, and might serve to prevent collisions during high-speed locomotion in these nocturnal animals. This 'look ahead' behaviour would increase offset angles (Arkley et al. 2014) and decrease whisker span, which can be seen in Figure 3b, however, this relationship was not significant. Whisker span, therefore, is probably associated with a number of parameters, including both offset and whisker length.

While the foot placements always fell within the whisker field, it is worth bearing in mind that whiskers are a discrete set of point sensors, and that the positioning of a whisker tip might not necessarily coincide at exactly the same place as a footfall. Data collection was carried out within the first five minutes of the animals being introduced to the experimental arena, this is an exploration phase where the animals locomoted forwards with their heads down to explore the floor, and only raised their heads to better investigate objects or vertical surfaces (Grant et al. 2009). Locomoting with their head down enables a large number of whisker contacts (see Figure 6, left, in Grant et al. 2009, and Figure 1a in Arkley et al. 2014) and increases the likelihood of a whisker contact coinciding in space with a foot placement.

The head was positioned downwards towards the floor in the majority of our data collection. Raising the head, as occurs during running and habituation to an environment (Arkley et al. 2014), lifts the smaller whiskers off the floor and enables floor contact only at the tips of the longer whiskers, with no contact beneath the snout (see Figure 6, right, in Grant et al. 2009, and Figure 1b and c in Arkley et al. 2014) . This head raising is associated with the look-ahead strategy, focussing the whiskers to detect impacts in front of the snout, rather than beneath it. Understanding how whisker layout, length and positioning affects whisker contacts with the ground, especially on small structures such as branches, would be an interesting direction for future work.

Longer whiskers are associated with small, nocturnal, arboreal mammals (Muchlinski et al. 2013). We can see in our data that the arboreal mammals tended to have relatively longer whiskers (especially *Rattus norvegicus, Muscardinus avellanarius* and *Apodemus sylvaticus*), with the terrestrial, diurnal *Cavia porcellus* having the smallest whiskers, and the semi-aquatic species (*Arvicola amphibius* and *Neomys fodiens*) being somewhat intermediary (Supplementary Material, Supplement 2). Similarly, climbing rodents have longer digits and higher joint mobility than semi-aquatic rodents (Samuels and Van Valkenburgh 2008), to enable good grasping during climbing. Having longer whiskers might ensure that the placement of these long, flexible digits can still be guided by whisker touch in arboreal mammals. We can also see in our data that the diurnal semi-aquatic *Arvicola amphibius* and *Neomys fodiens*, have shorter whiskers, and hence smaller whisker spans. Semi-aquatic rodents tend to have smaller forepaws than arboreal rodents, but larger hind limbs for paddling (Samuels and Van Valkenburgh 2008). Therefore, their smaller whisker span should be sufficient for guiding their smaller forepaws, although the semi-aquatic nature of their lifestyle may also be impacting on whisker length, for instance, longer whiskers may be harder to control in water. The terrestrial *Cavia porcellus* appears to have the smallest whiskers, relative to the other species examined here. It would be interesting to further explore how whisker length is associated with quadrupedal locomotion strategies and skeletal structures in a larger number of small mammal species. For example, the hip width of all the species here, are wider than the shoulder widths (Supplementary Material, Supplement 2). Therefore, the hind limbs may well naturally have a wider stance than the forelimbs, and be positioned outside of the whisker field, especially in animals with shorter whiskers, such as *Arvicola amphibius, Neomys fodiens* and *Cavia porcellus.*

Whisker movement and control

All of the species in this study whisked bar one. The exception was the diurnal, terrestrial *Cavia porcellus* which could only make unilateral whisker twitches, agreeing with previous observations of *Cavia porcellus* whisker movements (Jin et al. 2004; Grant et al. 2017). In the whisking species, whisker movements had clear protraction (forward) and retraction (backward) phases in all the animals apart from *Neomys fodiens*, where only retractions were present. Whisking is often more associated with nocturnal and arboreal species, although terrestrial and diurnal species can also whisk (Arkley et al. 2014; Grant et al. 2017; Muchlinski et al. 2018). In this study, the largest whisker movements, with the highest amplitudes, were observed in *Rattus norvegicus* and *Apodemus flavicollis*, which are both arboreal species (although they also burrow and run on the ground). Whisking is thought to enable rapid sampling during spatial exploration (Knutsen, 2015) and is associated with larger infraorbital nerves and higher tactile sensory acuity in small mammals (Muchlinski et al. 2018), which may well be important for tactually guiding climbing in complex environments, such as trees and hedgerows. Many of the arboreal species in this study engaged in all of the tested control strategies, including *Muscardinus avellanarius, Apodemus sylvaticus, Apodemus flavicollis, Rattus norvegicus* and *Micromys minutus*. Semi-aquatic mammals have highly sensitive whiskers (Dehnhardt et al. 1999), and we do see that *Arvicola amphibius* and *Neomys fodiens* engaged in many control behaviours, such as spread reduction and whisking. The terrestrial, diurnal *Cavia porcellus* engaged in the fewest control behaviours. Therefore, our data supports the idea that whisker-use is associated with complex habitats, including arboreal and aquatic environments.

As well as variations in whisking movements, aspects of whisker control also differed between species. Extensive studies in House mice (*Mus musculus*) and Brown rats (*Rattus norvegicus*) have revealed that whisker movements can be actively controlled during locomotion and object exploration. During object exploration, rats reduce the spacing, or spread, of their whisker, so that they bunch up on a surface and enable more whisker contacts (Grant et al. 2009; 2013). This behaviour is absent in the Grey short-tailed opossum, *Monodelphis domestica*, which lacks the muscular control to enable spread reduction (Grant et al. 2013). Our data found no evidence of this behaviour in *Suncus etruscus, Neomy fodiens* and *Cavia porcellus*. The absence of spread reduction in M. domestica and other small mammals suggests that it may have evolved after whisking accompanied by some changes in the whisking musculature (Grant et al. 2013; Muchlinski et al. 2018). Asymmetry, or more specifically contact-induced asymmetry (CIA), also often occurs following a unilateral contact and can be seen in *Mus musculus*, *Rattus norvegicus* and *Monodelphis domestica* (Mitchinson et al. 2011). It is characterised by the whiskers contralateral to the contact increasing in amplitude and the whiskers ipsilateral to the contact decreasing in amplitude, enabling asymmetry between the two whisker fields. In our data, we saw no evidence of this behaviour in *Suncus etruscus, Sorex minutus* and *Arvicola amphibius*. CIA appears to allow animals to increase the number of contacts with vertical surfaces of interest (Mitchinson et al., 2007), Since Mitchinson et al. (2011) found evidence of bilateral CIA in the marsupial opossum, *M. domestica*, it may have been present in early mammals, in which case it may have been lost in some modern-day species. The relationship between lifestyle and the ability to express different forms of CIA may be worth investigating further in different mammalian species, for example, the semi-aquatic lifestyle of *Sorex minutus* and *Arvicola amphibious* may explain some changes in aspects of whisker control.

Conclusions

Our data demonstrate that many small mammals use their whiskers to tactually guide safe foot positioning. Specifically, we have demonstrated that forepaw placement always falls within the whisker field of all the small mammals tested here, and that forepaw width is always smaller than whisker span. We have also demonstrated that nocturnal, arboreal and semi-aquatic mammals all show elements of active whisker control during object exploration and locomotion with arboreal mammals having the longest whiskers and full ability to control whisker spread and contact asymmetry. Overall, we propose that guiding locomotion, along with environment exploration, might be common functions of whisker touch sensing in small non-flying mammals.

Ethics Statement

All procedures were purely observational and therefore approved by the UK Home Office, under the terms of the UK Animals (Scientific Procedures) Act, 1986, and consistent with ethical guidelines at Manchester Metropolitan University (MMU), University of Sheffield, and approved by the local ethics committees at the Wildwood Trust and Bernstein Center for

Computational Neuroscience. All procedures complied with general handling and husbandry guidelines at the Wildwood Trust; animals were handled by Wildwood Trust Staff who had appropriate licenses, especially for dormice handing.

Data Accessibility

Data is shown as mean and standard deviation values in the Table 1 in the main text and in Supplement 2 and 4. All raw data is available on Dryad (doi:10.5061/dryad.92t4802).

Competing Interests

We have no competing interests.

Authors' Contributions

RG conceived the study, carried out the data collection, analysis and wrote the paper. VB supported data collection and manuscript drafting. TP Supported the conception of the study. All authors gave final approval for publication.

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FIGURES

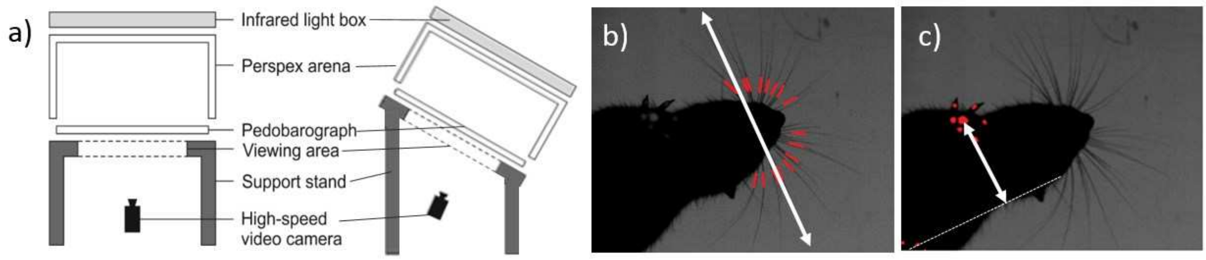


Figure 1: Filming set-up and example video stills. a) left: a diagram of the experimental arena. Animals could be filmed from below (when the pedobarograph was on) and from above (if the pedobarograph was not used). The experimental arena could also be tilted by 10 degrees to examine

locomotion and whisking on an inclined plane.(a, right) b) An example video still showing the whiskers and tracking; c) the same video-still with the foot placements indicated in red. The white lines show the whisker span (b) and forepaw width (c).

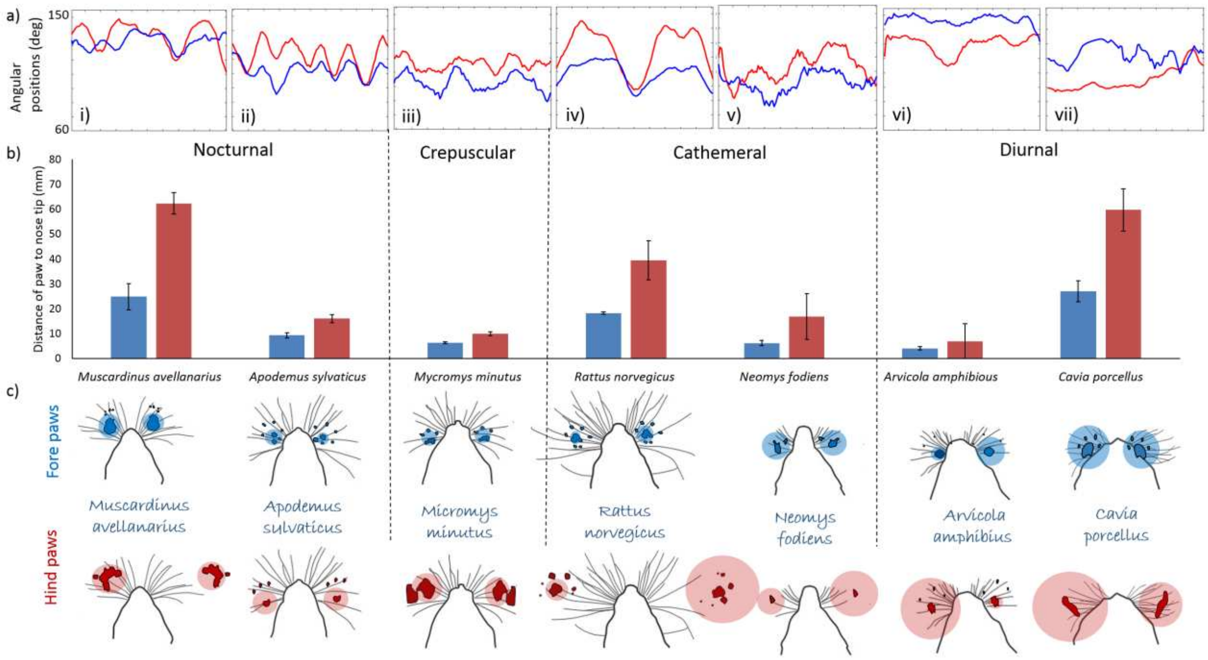


Figure 2. Whisker movements and paw placements in small mammals. a) example mean whisker angular position traces (60-150 degrees) over 200 ms for the left (in blue) and right (in red) whiskers for each of the species tested with a pedobarograph. b) bar charts showing the mean distance (with standard error bars) of paw placement from previous nose tip positions, for the forepaws (in blue) and hind paws (in red). c) diagram of traced footprints and a projection of their positioning on the whisker field, with approximated mean forepaw positions (in bold) and standard deviations (in lighter shading), for each species. The whiskers scan ahead of paw placements and this diagram shows the locations that the head has been in and the feet have moved in to. Forepaw placements always fall within the whisker field. Hind paw placements are more variable, but often fall within the whisker field.

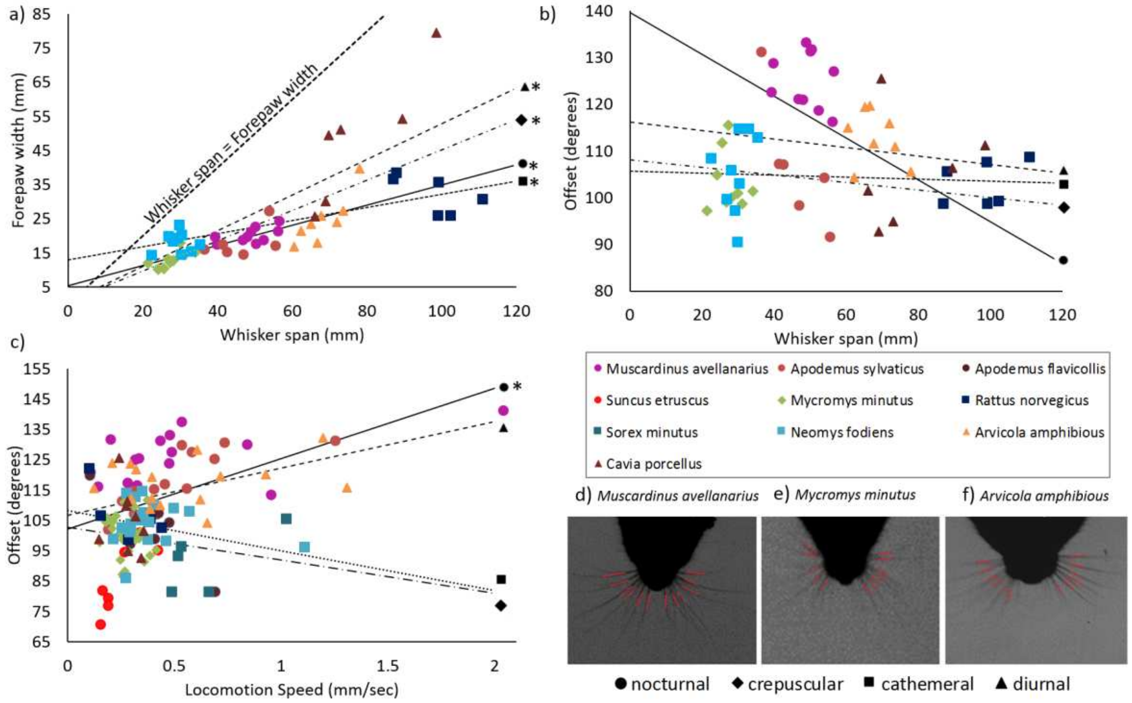


Figure 3 Whisker span and position are associated with elements of locomotion. a) Forepaw width was correlated to whisker span in diurnal, cathemeral, crepuscular and nocturnal species, and was always smaller than the whisker span in all of the species tested. b) Forepaw width was not correlated to offset values. c) Offset was correlated to locomotion speed in nocturnal species, but not in diurnal, crepuscular or cathemeral species. d-f) Screen shots of *Muscardinus avellanarius*, *Micromys minutus* and *Arvicola amphibious* at maximally protracting their whiskers during a period of fast locomotion. *Muscardinus avellanarius* has more forward protracting whiskers, with higher offset values. Graphs show individual species (in colour), with diurnal (triangle), cathemeral (square), crepuscular (diamond) and nocturnal (circle) indicated by different shapes. Linear line of best fit were plotted though the scatter plots for diurnal (triangle, dashed line), cathemeral and crepuscular (square, dotted line, both grouped here), and nocturnal (circle, full line) species groupings.

Supplementary Material

Supplement 1: The number of individuals filmed during the study, and the number of collected clips.

Common Name	Scientific Name	Activity pattern	Substrate preference	Filmed above	Filmed below[1]	No. individuals	No. clips collected	No. Clips Used
Hazel dormouse	*Muscardinus avellanarius*	Nocturnal	Arboreal	X	X	9	103	22
Etruscan shrew	*Suncus etruscus*	Nocturnal	Arboreal	X		6	106	7
Wood mouse	*Apodemus sylvaticus*	Nocturnal	Arboreal	X	X	5	71	18
Yellow-necked mouse	*Apodemus flavicollis*	Nocturnal	Arboreal	X		2	36	6
Harvest mouse	*Mycromys minutus*	Crepuscular	Arboreal	X	X	8	86	46
Brown rat	*Rattus norvegicus*	Cathemeral	Arboreal	X	X	6	54	10
Water shrew	*Neomys fodiens*	Cathemeral	Semi-aquatic	X	X	9	105	31
Pygmy shrew	*Sorex minutus*	Cathemeral	Terrestrial	X		2	60	5
Water vole	*Arvicola amphibious*	Diurnal	Semi-aquatic	X	X	7	77	26
Bank vole	*Myodes glareolus*	Diurnal	Terrestrial	X		1	12	2
Guinea pig	*Cavia porcellus*	Diurnal	Terrestrial	X	X	4	70	13
TOTAL:						59	780	

1. If filmed from below, also used the pedobarograph, and included being tested on the flat and inclined floor. Both whiskers and feet were measured in these species.

Supplement 2: Measurements extracted from the manually tracked footage.

Relative whisker lengths and forepaw widths in all the species tested, with geometric mean (GM = √(head width x head length). Hip width divided by shoulder width. Gait cycle and the minimum time of nose position to forepaw placement. Values are mean ± s.d.

Species	**Rel. Whisker lengths**	**Rel. Forepaw Widths**	**Geometric Mean (mm)**	**Hip/Shoulder width**	**Gait Cycle (Hz)**	**Min time of forepaw to nose (ms)**
Muscardinus avellanarius	2.15±0.26	0.90±0.10	22.65±2.09	1.01±0.04	2.09±1.96	223.01±201.56
Apodemus sylvaticus	2.24±0.36	0.88±0.23	20.57±1.31	1.23±0.09	3.12±0.55	88.10±12.24
Micromys minutus	1.69±0.23	0.81±0.15	16.36±1.77	1.07±0.10	4.26±0.38	47.00±5.22
Rattus norvegicus	2.83±0.26	0.94±0.16	34.53±0.76	1.22±0.06	1.76±0.01	225.58±20.78
Neomys fodiens	1.68±0.21	1.04±0.17	17.48±0.33	1.01±0.04	4.21±1.65	146.83±15.73
Arvicola amphibious	1.61±0.11	0.58±0.09	42.51±2.95	1.23±0.09	2.26±0.43	248.50±37.58
Cavia porcellus	0.88±0.15	0.54±0.22	88.44±4.13	1.24±0.11	5.00±0.00	366.25±143.25

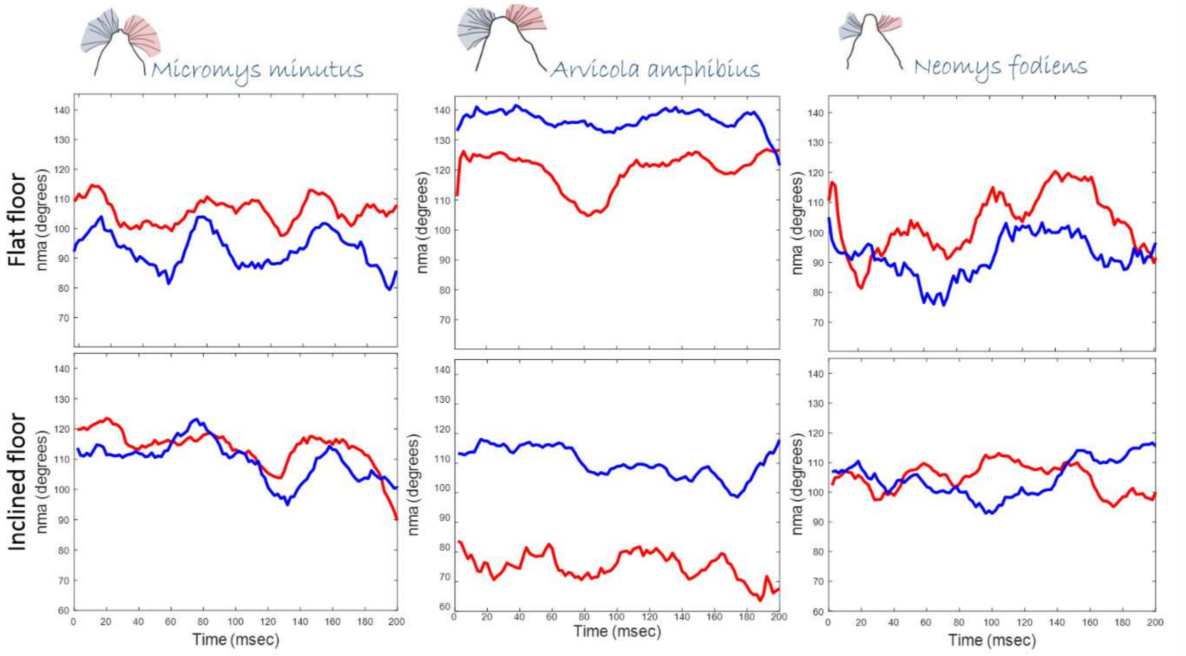
Supplement 3: Spearman's Rank correlation for offset, whisker span and forepaw width in nocturnal, crepuscular, cathemeral and diurnal mammals. Asterisks (*) refer to significant correlations, p<0.05.

Species	**Whisker Span vs. Forepaw Width**	**Whisker Span vs. Offset**	**Locomotion Speed vs. Offset**
Nocuturnal:			
Muscardinus avellanarius	R=0.552, p=0.027*	R=0.290, p=0.276	R=0.483, p=0.001*[a]
Apodemus sylvaticus			
Crepuscular:			
Micromys minutus	R=0.850, p=0.004*	R=0.000, p=1.000	R=-0.131, p=0.500
Cathemeral:			
Rattus norvegicus	R=0.693, p=0.004*	R=0.038, p=0.894	R=-0.263, p=0.160[b]
Neomys fodiens			
Diurnal:			
Arvicola amphibious	R=0.864, p<0.001*	R=-0.165, p=0.573	R=0.292, p=0.148
Cavia porcellus			

a. As well as the species mentioned, also includes data from *Apodemus flavicollis* and *Suncus etruscus* in the locomotion speed and offset correlation.
b. As well as the species mentioned, also includes data from *Sorex minutus* in the locomotion speed and offset correlation.

Supplement 4: Whisker measurement results for each species locomoting on an inclined floor. Asterisks indicate a significant difference to the flat floor data in that variable. Values are mean ± s.d.

Species	Loco Speed m/sec	Freq Hz	Off deg	Amp deg	Asym deg	Pro Speed deg/ms	Re Speed deg/ms
Muscardinus avellanarius	0.26±0.11	11.5±4.06	121.99±4.45	25.22±7.93	12.66±4.45	1.31±0.09*	0.10±0.08
Apodemus sylvaticus	0.34±0.26	16.08±7.05	117.28±10.09*	36.57±7.26*	11.95±3.78	1.48±0.14*	0.37±0.23
Mycromys minutus	0.33±0.14	12.88±6.44	102.10±5.41	34.49±8.75**	14.34±8.75*	1.60±0.22**	0.29±0.09**
Rattus norvegicus	0.32±0.14	10.13±2.29	99.39±12.48	29.44±8.98	14.34±3.43	1.25±0.04*	0.08±0.02*
Neomys fodiens	0.39±0.08	12.55±6.76	102.35±6.32	29.37±4.33**	12.18±2.07**	1.53±0.10	0.22±0.05*
Arvicola amphibious	0.61±0.24	9.55±1.56	114.73±7.27	26.54±12.51*	27.17±8.66	1.56±0.70	0.09±0.10*
Cavia porcellus	0.32±0.06	n.a.	106.60±16.99	49.30±24.45	30.72±23.52	n.a.	n.a.



Supplement 4, Figure 1. Example mean whisker angle traces from the left (in blue) and right (in red) whisker field from three species locomoting on an inclined floor. Significant reductions could be observed in whisker amplitude when the animals were locomoting on the inclined floor, compared to the flat floor.