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Corresponding Author:	Tony J Prescott, MA MSc PhD University of Sheffield Sheffield, South Yorkshire UNITED KINGDOM
First Author:	Kendra Arkley, BSc
Order of Authors:	Kendra Arkley, BSc
	Robyn A Grant, BSc PhD
	Ben Mitchinson, BSc PhD
	Tony J Prescott, MA MSc PhD
Abstract:	During exploration, rats, and other small mammals, make rhythmic back and forth sweeps of their long facial whiskers (macrovibrissae). These "whisking" movements are modulated by head movement, and by vibrissal sensory input, and hence are often considered "active" in the Gibsonian sense of being purposive and information-seeking. An important hallmark of active sensing is the modification of the control strategy according to context. Using a task in which rats were trained to run circuits for food, we tested the hypothesis that whisker control, as measured by high-speed videography, changes with contextual variables such as environment familiarity, risk of collisions, and availability of visual cues. In novel environments, functionally-blind rats moved at slow speeds and performed broad whisker sweeps. With greater familiarity, however, they moved more rapidly, protracted their whiskers further and showed decreased whisking amplitude. These findings indicate a strategy change from using the vibrissae to explore nearby surfaces, to using them primarily for 'look-ahead'. In environments with increased risk of collision functionally-blind animals moved more slowly but protracted their whiskers further. Sighted animals also showed changes in whisker control strategy with increased familiarity, but different to those of the functionally-blind strain, for instance increasing rather than decreasing whisk amplitude with increasing familiarity. Sighted animals also changed their vibrissal behavior when visual cues were subsequently removed (by being placed in darkness). These contextual influences provide strong evidence of active control and demonstrate that the vibrissal system provides an accessible model of purposive behavior in mammals.

THE UNIVERSITY OF SHEFFIELD

Department of Psychology

® *Head of Department: Professor Paul Overton*

Psychology Building
Western Bank
Sheffield S10 2TP – UK
Tel: +44 114 222 9272
Fax: +44 114 276 6515
http://www.shef.ac.uk/psychology/

Prof. Tony Prescott   44 114 222 6547   **http://www.shef.ac.uk/~abrg/tony**   **T.J.Prescott@sheffield.ac.uk**

Geoffrey North,
Editor, Current Biology

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Re: Ms. No. CURRENT-BIOLOGY-D-13-00675

Dear Dr North,

Many thanks for accepting our paper for publication in *Current Biology*. As the reviewers made no additional comments, we have now uploaded our report and all necessary documents. The supplemental information and all figures have been optimized according to style requirements, and we wish to pay the fee for all four color figures.

Yours sincerely,

Professor Tony Prescott, Corresponding Author.

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Response to Reviewers

We thank both reviewer #1 and #2 for the time and effort they have given to reading our revised manuscripts. Our accepted article is much stronger as a result of their detailed and thoughtful comments.

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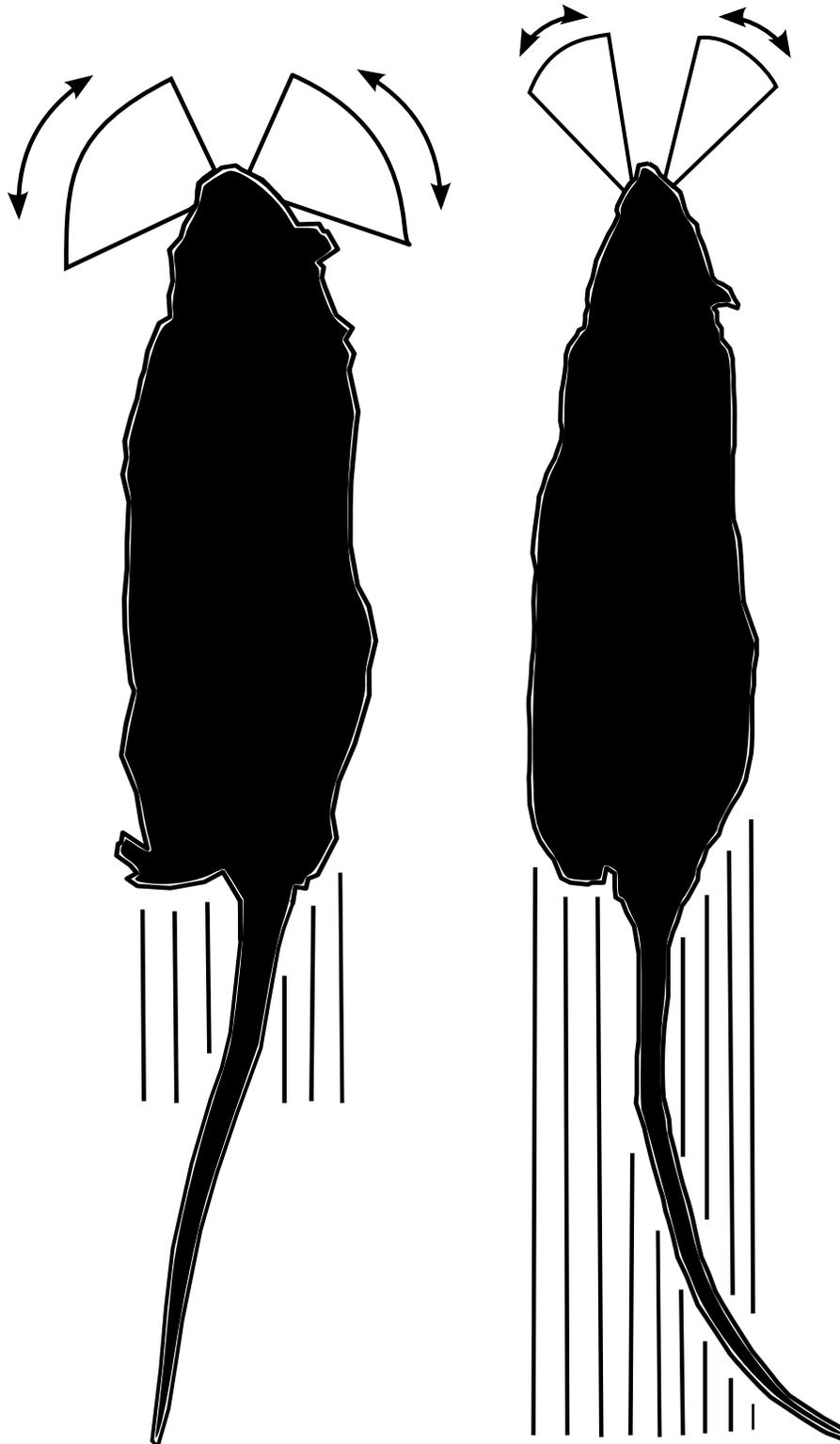
Strategy change in vibrissal active sensing during rat locomotion

Kendra Arkley[1], Robyn A. Grant[2], Ben Mitchinson[1] and Tony J. Prescott[1]*

[1]Active Touch Laboratory, Department of Psychology, University of Sheffield, Western Bank,

Sheffield, S10 2TN, UK

[2]Conservation, Evolution and Behaviour Research Group, Division of Biology and Conservation

Ecology, Manchester Metropolitan University, Chester Street, Manchester, M1 5GD, UK

*corresponding author: t.j.prescott@sheffield.ac.uk, phone: +44 114 2226547, fax: +44 114 2766515

Running head: Strategy change in vibrissal active sensing

Highlights

- Rats purposefully change their whisker position according to environment familiarity

- A 'look-ahead' whisker strategy is adopted when running at fast locomotion speeds

- With risk of collisions, rats decrease their speed and increase whisker look-ahead

- Visual input alters the relationship between whisker control and locomotion speed

Summary

During exploration, rats, and other small mammals, make rhythmic back and forth sweeps of their long facial whiskers (macrovibrissae) [1-3]. These "whisking" movements are modulated by head movement [4], and by vibrissal sensory input [5-6], and hence are often considered "active" in the Gibsonian sense of being purposive and information-seeking [7-8]. An important hallmark of active sensing is the modification of the control strategy according to context [9]. Using a task in which rats were trained to run circuits for food, we tested the hypothesis that whisker control, as measured by high-speed videography, changes with contextual variables such as environment familiarity, risk of collisions, and availability of visual cues. In novel environments, functionally-blind rats moved at slow speeds and performed broad whisker sweeps. With greater familiarity, however, they moved more rapidly, protracted their whiskers further and showed decreased whisking amplitude. These findings indicate a strategy change from using the vibrissae to explore nearby surfaces, to using them primarily for 'look-ahead'. In environments with increased risk of collision functionally-blind animals moved more slowly but protracted their whiskers further. Sighted animals also showed changes in whisker control strategy with increased familiarity, but different to those of the functionally-blind strain, for instance increasing rather than decreasing whisk amplitude with increasing familiarity. Sighted animals also changed their vibrissal behavior when visual cues were subsequently removed (by being placed in darkness). These contextual influences provide strong evidence of active control and demonstrate that the vibrissal system provides an accessible model of purposive behavior in mammals.

Results

We examined the relationship between whisking kinematics and locomotion speed in seven functionally-blind (retinally dystrophic) rats that were trained, over several days, to run circuits of an experimental arena for food. As illustrated in Figure 1 (see also Movies S1, S2, and S3) these animals increased their forward locomotion speed over the course of training—divided into early, intermediate and late stages—(and into speed categories, see Figure S1) consistent with earlier investigations of rat locomotion in novel environments [10-12]. Using high-speed videography (recorded in two views)

and automated whisker tracking we were able to quantify aspects of the animals' whisking kinematics despite their rapid speed of locomotion. We found that as animals gained increased familiarity with the environment, and moved more quickly, they also altered their whisker movements, changing from broad exploratory whisking sweeps directed at nearby surfaces, including the floor, to a strategy of protracting the whiskers further in front of the snout (increasing whisker *set-point*), and significantly reducing the amplitude and frequency of back-and-forth whisker motion—as the animal moves faster the whisker movement and positioning thus appears to adapt so as to provide improved *looked-ahead* in the direction of travel (see Figure 2 and Figure S1, condition 1 for histograms and significance levels; see Table S1 for additional statistical details).

The change in whisker movement with increasing environment familiarity could potentially be as the result of a direct relationship between speed of locomotion and whisker control, as might be mediated, for instance, by reflexive mechanisms. To determine whether or not this was the case we examined the effect on whisker movement of changing expectations about the likelihood of unexpected collisions. Specifically, we trained a second group of three functionally-blind animals (condition 2) to run circuits in an arena where obstacles, in the form of cuboid metallic pillars, appeared at unpredictable times and location. In this group we saw reduced locomotion speed, compared to animals faced with a fixed environment, alongside significantly greater protraction of their whiskers (increased set-point) and reduced whisk amplitude (all $p < .001$, see Table S1 for statistical details). These differences are consistent with an increased emphasis on *collision-detection* when faced with unpredictable changes in obstacle locations, with animals moving more slowly and directing their spatial attention more strongly towards the direction of travel when there is a higher collision risk.

The functionally-blind animal allows us to examine whisker control in rats that are required to rely on vibrissal touch as their primary way to discover environmental structure, however, what happens when animals are able to combine tactile and visual cues? To investigate this question we repeated our experiment using sighted animals, weight-matched to those of the functionally-blind strain, and including both fixed environment and moving obstacle conditions (respectively condition 3, $N = 4$ and condition 4, $N = 5$).

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A multivariate ANOVA with follow-up tests was performed on data from groups 1–4, showing significant main effects of expectations about obstacles and the availability of visual cues on running speed (η_p^2 = .05, .39), whisker protraction set-point (η_p^2 = .03, .08), amplitude (η_p^2 = .06, .18, all $p <$ 0.001) and frequency (η_p^2 = .006, .54; $p < 0.05$), and a significant interaction whereby unsighted and sighted animals responded differently to increased risk of collision, with respect to both whisker set-point (η_p^2 = .05) and locomotion speed (η_p^2 = .008; both $p < 0.001$), but not amplitude (η_p^2 = .003; $p =$ .092). As shown in Figure 2 sighted animals, in both conditions 3 and 4 ran faster than the functionally-blind animals, and increased their locomotion speed much more over the course of training, whilst showing a significant change in head lift (from head-down to parallel with the floor). Similar to the unsighted animals, they also showed a significant increase in whisker set-point with increasing familiarity/running speed and reduction in whisk frequency (although from a higher starting frequency). Interestingly, whereas the functionally-blind animals reduced whisk amplitude with training, the sighted animals significantly *increased* whisk amplitude. The whisking behavior of sighted animals was also differently affected by the presence of moveable obstacles—although sighted animals did move more slowly in condition 4, they did not show any further increase in whisker protraction, in contrast, head lift and whisk amplitude appeared to be influenced by the presence of unexpected obstacles with animals adopting a more elevated head position and higher whisk amplitude in the initial phase of training in the environment with greater collision risk. Figure 3 illustrates the interaction of risk of collisions and presence of visual cues on whisker set-point and locomotion speed.

To better understand the role of visual cues, sighted animals from conditions 3 and 4 were further trained for three days under the same experimental settings (i.e. with or without obstacles), but in a darkened arena under infrared illumination. Looking at behavior on the first day of training in darkness, we found that rats in both conditions reduced their running speed and whisking kinematics to be similar to that displayed at the intermediate stage of training under light (Figure 2). Thus loss of visual cues appeared to reduce these animals confidence to run through the arena very quickly and they made some adjustment to whisker control accordingly.

Since we found that rats push their whiskers further forward as they go faster, we wished to examine how much additional response time such a strategy can provide, and how much this might assist the animal in avoiding, or reducing the impact of, collisions with obstacles. Focusing on 133 randomly selected video clips from the dataset in condition 2 (unsighted/obstacles), we estimate (see Supplemental Experimental Procedures) that by increasing whisker set-point rats were able to provide themselves with an average *tactile look-ahead distance* (TLD; distance from snout-tip to whisker-tip) of 24.6 mm (SD = 3.7 mm) compared to 18.6 mm (SD = 0.3 mm) for an exploratory whisking strategy (mean of eight video clips from the early training stage of condition 1). Using the locomotion speed from each selected clip we computed *time-to-collision* (TTC; time between whisker-tip contact and subsequent snout-tip collision) which averaged 62 ms (SD = 16 ms) when using a look-ahead strategy, compared to 48 ms (SD = 13 ms) when using an exploratory strategy. We also found that TTC marginally decreased with increased running speed (r = –.171, p = .048; see Figure S2), as might be expected, but not as rapidly as it would without the compensation of increased whisker protraction. Sighted animals running with more protracted whiskers also gain some benefit in increased TTC (see Supplemental Experimental Procedures for details).

The functional significance of additional TTC, for the unsighted animals at least, can be expressed as an opportunity for the animal to achieve greater deceleration (or stop/swerve) before colliding with an obstacle as illustrated in the sequence of example video frames shown in Figure 4 (see also Movie S2). In 57 video clips from condition 2 in which animals showed rapid braking following whisker tip contact we calculated the deceleration rate 48 ms and 62 ms after initial whisker contact with the obstacle (the TTCs when adopting typical exploratory, 48 ms, or look-ahead, 62 ms, whisker control strategies). As shown in Figure 4, this analysis indicated that average forward locomotion velocity typically decreases by 31% between contact and +48 ms, with look-ahead TTC (+62 ms) providing an *additional* 24% (55% overall) decrease in forward locomotion compared to the velocity at whisker-tip contact. This result indicates that additional whisker protraction during fast running does provide some safety benefit for the animal in allowing more time to adjust running speed and trajectory, increasing the likelihood of collision avoidance or reducing speed at collision. For further information regarding

the total amount of high-speed video data collected and analyzed per condition and animal, see Supplemental Experimental Procedures.

Discussion

We have found that rats modify their use of the macrovibrissae for guidance of locomotion depending on their familiarity with the environment, the likely risk of collisions, and the presence of visual cues. More specifically, we have found a relationship between familiarity and whisker movements, such that in unfamiliar environments, whilst moving at slower running speeds, functionally-blind rats engage in a more exploratory whisking style involving broad whisker sweeps and allowing a detailed tactile investigation of the substrate, consistent with a potential role for the whiskers in detecting surface properties and in identifying secure places for footfalls. In contrast, during high-speed locomotion in familiar environments, these rats adopt a more 'look-ahead' strategy—holding their heads higher and more parallel with the floor, and significantly protracting their whiskers in front of the snout whilst decreasing the amplitude of whisking. This strategy affords additional response time in the case of an unexpected object contact, potentially allowing the animal to maneuver so as to avoid a collision, or to stop and orient to an object of interest. These different strategies are not dichotomous, rather the behavior of the animal appears to lie on a continuum with strongly exploratory behavior at one end, and primarily look-ahead behavior at the other, and with locomotion speed a significant factor but not the sole determinant (see Figure S4 and Table S2 for partial correlations of these and other trends). This shift can be understood as adaptive since stopping distance is greater during fast locomotion, collisions at speed can be damaging to the animal, and protracted whiskers can give early warning of any unexpected obstacles that may lie in the animal's path.

Whilst a relationship between locomotion speed and whisking kinematics is displayed robustly in both conditions 1 and 2 (functionally-blind animals with/without obstacles), the differences between the two conditions further support the hypothesis that changes in whisker behavior reflect an adaptive shift in the type of information being sought by the animal. In particular, the more pronounced look-ahead strategy of functionally-blind animals faced with unpredictable changes to their environments (condition 2) strongly suggests a role of expectations in determining the relationship between

whisking style and locomotion, and argues against any simple reflexive mechanism such as a straight-forward mapping from locomotion variables to whisker control. In this condition, animals *moved more slowly* compared to when the environment was fixed, and yet they *protracted their whiskers more* (Figure 3), so the mechanism mediating the interaction between locomotion and whisking must be able take into account the broader context, including obstacles that cannot be immediately sensed but can be expected based on recent experience. We infer that unsighted rats proceed more cautiously when they perceive higher risk, moderating their running speed and increasing their whisker look-ahead distance based on recent experience of unpredictable obstacles in order to reduce collision risk. Indeed, a large number of video clips from condition 2 show whisker-obstacle contacts (367/606) with the majority of those contact events being immediately followed by orienting movements towards the obstacle (203/367 high-speed clips) which is consistent with the object contacts being unexpected, and the input from the whiskers being important for obstacle detection (see Figure 4).

The differences between sighted and functionally-blind strains further confirms that there is a relatively complex relationship between locomotion and vibrissal sensing, mediated, in part, by the availability of cues from other modalities. Sighted animals run at much higher locomotion speeds than unsighted individuals (top speeds of around 150 cm/s compared to 100 cm/s) in lit conditions but slow down again when placed in darkness; these data strongly imply that the availability of visual cues allows animals to proceed with less caution. Nevertheless, sighted rats also exhibited a clear whisker look-ahead strategy when moving at speed even under good illumination. Rats are known to have poor visual acuity [13-14] and lack continuous binocular fusion [15], so although vision can provide early warning of obstacles in these conditions it is possible that touch provides more accurate TTC information than vision at close range such that visual obstacle avoidance is usefully complemented by touch. Interestingly, sighted animals show an opposite relationship between whisk amplitude and running speed to functionally-blind animals, increasing rather than reducing amplitude as they move faster. This difference was unexpected and would warrant further investigation. The relationship is further complicated by the observation that in condition 3 (sighted/no obstacles), at the early stage of training and when moving slowly, sighted rats showed lower amplitude whisking than in all other

conditions, which could be interpreted as showing that under light, and in this simple and unchallenging environment, sighted animals may make less use of their vibrissal sense.

On a cautionary note, it should be acknowledged that some differences observed between the sighted and functionally-blind animals studied here could also be due to strain differences (we used sighted Hooded Lister compared to retinally dystrophic functionally-blind RCS animals), in particular, although weight matched, the Hooded Lister animals were younger, perhaps contributing to their higher maximum locomotion speeds.

The use of the macrovibrissae appears to be important in different ways for slow exploratory walking and high-speed running. In the former case, animals move sufficiently slowly to allow inspection of the substrate using exteroception, and make multiple whisker contacts with the floor surface prior to footfalls. Thus, whilst there is only limited direct evidence that whisker touch guides foot placement in rodents (see below), considerable vibrissal sensory information does appear to be available to the animal that could allow it to do so. In contrast, during running, locomotion is more of an open-loop activity [16], and the evidence presented here also suggests significantly less contact of vibrissae with the substrate during running due to the raised head posture and reduced amplitude of whisker movement. Nevertheless, a number of the longer ventral (lower-row) whiskers do make prolonged contact with the ground even during fast running, suggesting that whiskers could have a role in the sensory guidance of locomotion regardless of speed. These functions could include detection of relevant substrate properties (height, orientation, slip, compliance), maintenance of equilibrium, and path integration.

Rat whisking emerges alongside walking during development, suggesting a close relationship between vibrissal sensing and the sensory guidance of locomotion [16-18]. The value of whiskers in complex locomotor tasks is also indicated by evidence that small arboreal mammals, particularly nocturnal ones, have longer macrovibrissae than similar ground-dwelling species [19-21] and that animals deprived of their vibrissae move more slowly and make more errors on an elevated maze [22]. Sokolov & Kulikov [21] analysed the tracks left by the whisker tips and feet of Jerboas (*Euchoreutes*

naso; Dipus sagitta) during walking, running and jumping on soot-covered paper. They found that the whisker tips almost continuously traced marks along the floor directly where the footfalls of the animal subsequently appeared (particularly when the animal jumped over a barrier). Thé et al. [23] have recently shown that the 'whisker trident' of the rat, a three-whisker array on the underside of the chin, drags along the ground during exploratory locomotion, and could provide information about heading direction and velocity. That the vibrissal sense can also serve to alert animals to unexpected obstacles is also interesting from a comparative perspective as tactile sensing as a method for obstacle-detection during high-speed running has also been shown in insects [24-25]. For instance, during fast locomotion, cockroaches (*Periplaneta Americana*) scan and follow walls with their antenna held still and pushed forward. As in the rat, this behavioral strategy appears to assist collision avoidance during rapid travel by increasing look-ahead distance [26]. More generally, modifications in active sensing due to context have also been investigated in electrosensory [27-28] and echolocating animals [29-30].

Changes in whisker control have been described in a number of previous studies of vibrissal active sensing. For instance, Carvell & Simons [31] described how animals trained to discriminate texture held some of their more rostral whiskers stationary and in contact with the target surface, whilst moving their more caudal whiskers over the surface. Zuo et al. [32] have also described individual differences in whisker control strategies of animals trained in texture discrimination. Berg and Kleinfeld [33] contrasted exploratory whisking (as described here) with what they termed the "foveal" whisking observed when animals investigated a specific stimulus object such as a food spout. Foveal whisking, shares increased whisker protraction (set-point) with the look-ahead whisker control described here, but differs in that strong high-frequency oscillations of the whiskers are also present. Grant et al. [6] also described an increase in whisker set-point accompanied by a decrease in the angular spread of the whiskers when animals investigate surfaces, though, again, the animals continued to perform exploratory whisking sweeps. Whilst reporting evidence of changes in whisker control, none of these studies specifically sought to analyze strategy change and therefore did not include controls to determine whether these modifications in whisker kinematics were purely stimulus-driven. The current study shows clear evidence of the modulation of whisking strategy by the

broader context including expectations about the complexity of the environment and the availability of information from other sensory modalities. We have thus provided new evidence that vibrissal touch is purposive and information-seeking, in other words, that it bears the essential hallmarks of an active sensing system.

Experimental procedures

The study was conducted at the Active Touch Laboratory at the University of Sheffield (ATL@S), UK and in accordance with the Animals (Scientific Procedures) Act, 1986. Experimental animals were ten adult dystrophic (functionally-blind) Royal College of Surgeons (RCS) rats (used in conditions 1 and 2) and nine adult, sighted Hooded Lister (HL) rats (used in conditions 3 and 4). Animals were served a restricted diet in order to motivate them to run the arena for food reward, during which, high-speed video clips were taken of the animal travelling down the central corridor of our arena (see Supplemental Experimental Procedures for full details and Figure S3 for a photograph of setup), revealing both top-down and side-on views (latter via a mirror; see Figure 1). Each animal completed 30 minutes, or 40 cycles of the arena each day, until the learning criteria—at least three days of 40 cycles—was reached. In conditions 2 and 4, a metal cuboid object (50 x 50 mm x 100 mm; length, width, height) was placed into the central corridor in one of four possible locations adjacent to a sidewall, and moved pseudo-randomly to an alternate position every fifth cycle. In each session, a high-speed video clip of 1.6 seconds was recorded in every second cycle, using a manual trigger, until 12 clips in total had been recorded. Specific criteria for inclusion of high-speed video clips into the analysis (such as rotations of the head) were strictly adhered to (see Supplemental Experimental Procedures). In all clips that met these criteria the animal's whiskers and snout were tracked in the overhead view, and its snout in the side view, using the BIOTACT Whisker Tracking Tool (BWTT) [34]. For an overview of the total amount of high-speed video data collected and analyzed per condition and animal, see Supplemental Experimental Procedures. Using Fourier analysis, the animal's whisker kinematics (set-point, amplitude and frequency), locomotion speed, and position of the snout relative to the ground were computed using the tracked snout and whisker data. Non-parametric Kruskal-Wallace and Mann-Whitney U tests with a Bonferroni adjustment were used for

all statistical group comparisons, with the exception of a multivariate ANOVA to investigate the interaction between the expectation of obstacles and the availability of visual cues, and Pearson's partial correlation tests that were performed using bootstrapping (1000 iterations). All procedures and data analyses are described in more detail in the Supplemental Experimental Procedures.

References

1. Welker, W. I. (1964). Analysis of sniffing of the albino rat. Behav. 22, 223-244.

2. Wineski, L. E. (1983). Movements of the cranial vibrissae in the golden hamster (*Mesocritus auratus*). J. Zool. (Lond.) 200, 261-280.

3. Mitchinson, B., Grant, R. A., Arkley, K., Rankov, V., Perkon, I. and Prescott, T. J. (2011). Active vibrissal sensing in rodents and marsupials. Philos. Trans. Roy. Soc. B: Biol. Sci. 366, 3037-3048.

4. Towal, R. B. and Hartmann, M. J. (2006). Right-left asymmetries in the whisking behavior of rats anticipate head movements. J. Neurosci. 26, 8838-8846.

5. Mitchinson, B., Martin, C. J., Grant, R. A. and Prescott, T. J. (2007). Feedback control in active sensing: Rat exploratory whisking is modulated by environmental contact. P. Roy. Soc. Lond. B Biol. 274, 1035-1041.

6. Grant, R. A., Mitchinson, B., Fox, C. and Prescott, T. J. (2009). Active touch sensing in the rat: Anticipatory and regulatory control of whisker movements during surface exploration. J. Neurophysiol. 101, 862-874.

7. Gibson, J. J. (1962). Observations on active touch. Psychol. Rev. 69, 477-491.

8. Prescott, T. J., Diamond, M. E. and Wing, A. M. (2011). Active touch sensing. Philos. Trans. Roy. Soc. B: Biol. Sci. 366, 2989-2995.

9. Bajcsy, R. (1988). Active perception. Proc. IEEE 76, 996-1005.

10. Schmidt, A. and Fischer, M. S. (2010). Arboreal locomotion in rats – the challenge of maintaining stability. J. Exp. Biol. 213, 3615-3624.

11. Eilam, D. and Golani, I. (1988). The ontogeny of exploratory behavior in the house rat (*Rattus rattus*) the mobility gradient. Dev. Psychobiol. 21, 679-710.

12. Lelard, T., Jamon, M., Gasc, J. P. and Vidal, P. P. (2006). Postural development in rats. Exp. Neurol. 202, 112-124.

13. Birch, D., and Jacobs, G. H. (1979). Spatial contrast sensitivity in albino and pigmented rats. Vis. Res. 19, 933-937.

14. Prusky, G. T., Harker, K. T., Douglas, R. M. and Whishaw, I. Q. (2002). Variation in visual acuity within pigmented, and between pigmented and albino rat strains. Behav. Brain Res. 136, 339-348.

15. Wallace, D. J., Greenberg, D. S., Sawinski, J., Rulla, S., Notaro, G. and Kerr, J. N. D. (2013). Rats maintain an overhead binocular field at the expense of constant fusion. Nature 498, 65-69.

16. McNeill Alexander, R. (2003). Principles of animal locomotion (Princeton University Press).

17. Grant, R. A., Mitchinson, B. and Prescott, T. J. (2012). The development of whisker control in rats in relation to locomotion. Dev. Psychobiol. 54, 151-168.

18. Landers, M. and Zeigler, P. H. (2006). Development of rodent whisking: trigeminal input and central pattern generation. Somatosens. Mot. Res. 23, 1-10.

19. Ahl, A. S. (1986). The role of vibrissae in behavior: A status review. Vet. Res. Commun. 10, 245-268.

20. Ahl, A. S. (1987). Relationship of vibrissal length and habits in the Sciuridae. J. Mammal. 68, 848-853.

21. Sokolov, V. E. and Kulikov, V. F. (1987). The structure and function of the vibrissal apparatus in some rodents. Mammalia 51, 125-138.

22. Vincent, S. B. (1912). The function of the vibrissae in the behaviour of the white rat. Behav. Monogr. 1, 1-82.

23. Thé, L., Wallace, M. L., Chen, C., Chorev, E. and Brecht, M. (In press). Structure, function and cortical representation of the rat submandibular whisker trident. J. Neurosci.

24. Camhi, J. M. and Johnson, E. N. (1999). High-frequency steering maneuvers mediated by tactile cues: antennal wall-following in the cockroach. J. Exp. Biol. 202, 631-643.

25. Cowan, N. J., Lee, J. and Full, R. J. (2006). Task-level control of rapid wall following in the American cockroach. J. Exp. Biol. 9, 1617-1629.

26. Cowan, N. J., Ma, E. J., Cutkosky, M. and Full, R. J. (2005). A biologically inspired passive antenna for steering control of a running robot. Robotics Res. 541-550.

27. Cowan, N. J. and Fortune, E. S. (2007). The critical role of locomotion mechanics in decoding sensory systems. J. Neurosci. 27, 1123-1128.

28. Stamper, S. A., Roth, E., Cowan, N. J. and Fortune, E. S. (2012). Active sensing via movement shapes spatiotemporal patterns of sensory feedback. J. Exp. Biol. 215, 1567-1574.

29. Ghose, K. and Moss, C. (2006a). Steering by hearing: A bat's acoustic gaze is linked to its flight motor output by a delayed, adaptive linear law. J. Neurosci. 26, 1704-1710.

30. Yovel, Y., Falk, B., Moss, C. F. and Ulanovsky, N. (2011). Active control of acoustic field-of-view in a biosonar system. PloS Biol. 9, e1001150.

31. Carvell, G. E. and Simons, D. J. (1990). Biometric analyses of vibrissal tactile discrimination in the rat. J. Neurosci. 10, 2638-2648.

32. Zuo, Y., Perkon, I. and Diamond, M. E. (2011). Whisking and whisker kinematics during a texture classification task. Philos. Trans. Roy. Soc. B: Biol. Sci. 366, 3058-3069.

33. Berg, R. W. and Kleinfeld, D. (2003). Rhythmic whisking by rat: Retraction as well as protraction of the vibrissae is under active muscular control. J. Neurophysiol. 89, 104-117.

34. Perkon, I., Kosir, A., Itskov, P. M., Tasic, J. and Diamond, M. E. (2011). Unsupervised quantification of whisking and head movement in freely moving rodents. J. Neurophysiol. 105, 1950-1962.

Figure Legends

Figure 1. Evidence for a change in locomotion and whisking kinematics over the course of training. Example data showing typical runs from one animal in condition 1 (no obstacles) showing: (left) example high-speed video frames of rat body posture and whisker position in side-on and overhead views, (middle) example locomotion trajectory plots with scale, and (right) whisker traces indicating the per-frame smoothed mean angle of the whisker field and mean set-point (low-pass filter at 30 and 2 Hz). Training stage is shown from top to bottom. **A.** Early training. The animal walks slowly, in this case following a meandering path, head close to the ground and engages in strongly oscillatory exploratory whisking. **B.** Intermediate training. Locomotion speed has increased, the overall angle of the whiskers has becomes more protracted and whisk amplitude has decreased. The trajectory is less meandering. **C.** Late training. Locomotion speed is very fast, with head held high, long stride length, and, in this example, near straight-line travel. The whisker trace shows lower frequency and amplitude whisker movement with strong protraction (high set-point). See also Movie S1.

Figure 2. Histograms showing the effect of training stage (*familiarity*) – early (blue), intermediate (red), and late (green) training – on locomotion and whisking variables from conditions 1-4: unsighted/no obstacles, unsighted/obstacles, sighted/no obstacles, sighted/obstacles. Grey-scale bars represent the first day of further training under infrared light (conditions 3 and 4 only). A Kruskal-Wallis ANOVA was used to examine the overall effect of training stage and follow-up Mann-Whitney *U* tests with a Bonferroni adjustment ($\alpha = .025$) to examine discrete differences. Stars denote significance (* $p < .025$, ** p < .001). Medians are displayed, error bars show 95% confidence intervals. See also Figure S1 (effect of locomotion speed category on measured variables) and Table S1 for detailed statistics.

Figure 3. Evidence that the relationship between whisker control and locomotion speed is not mediated by simple reflexive mechanisms. Whisker set-point (top; $F_{(1,986)} = 129.84$, $p < .001$) and locomotion speed (bottom; $F_{(1,986)} = 7.77$, $p < .001$) are differently affected by likely risk of collisions in functionally-blind and sighted animals.

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Figure 4. An example of whisker-obstacle contact and subsequent slowing of rat locomotion from condition 2 (unsighted/obstacles). Whisker contact can allow an animal to detect an obstacle before a collision occurs. The increased whisker protraction of rats that use a look-ahead active sensing strategy therefore allows additional time for deceleration before collision—15ms on average in our data. A Kruskal-Wallis ANOVA was used to examine the overall difference between pre- and post-contact forward locomotion velocities and follow-up Mann-Whitney U tests with a Bonferroni adjustment ($\alpha = .017$) to examine discrete differences. As can be seen, forward locomotion velocity decreases significantly from the moment of initial whisker contact (0 ms), and between +48 and +62 ms after contact suggesting the 15 ms extra time to collision results in a substantial deceleration. Stars denote significance (* $p < .017$, ** $p < .001$). Error bars show standard error. See also Movie S2 for corresponding video clip and Figure S2 for additional TTC afforded using a look-ahead whisker strategy.

Figure 1

C Late training stage

B Intermediate training stage

A Early training stage

100 mm

Mean angle of the whiskers (°)

Time (s)

Left whisker field
Right whisker field

Left whisker field
Right whisker field

Left whisker field
Right whisker field
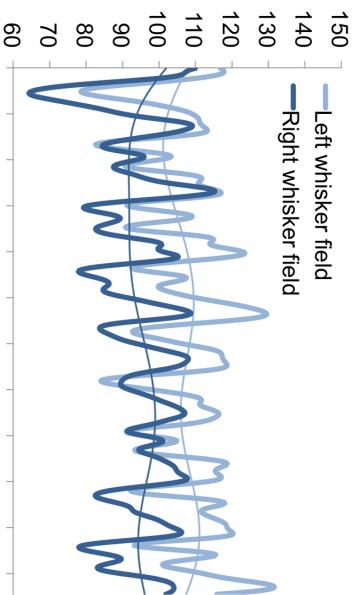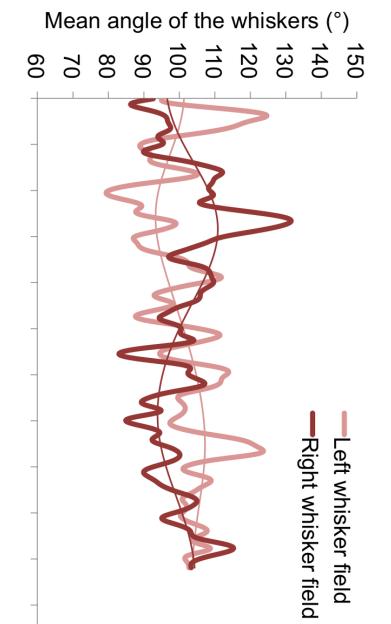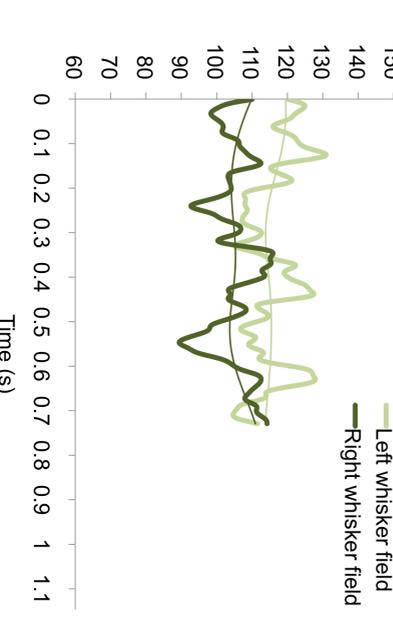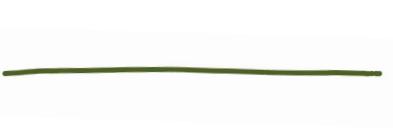
Figure 2

Head lift (mm)
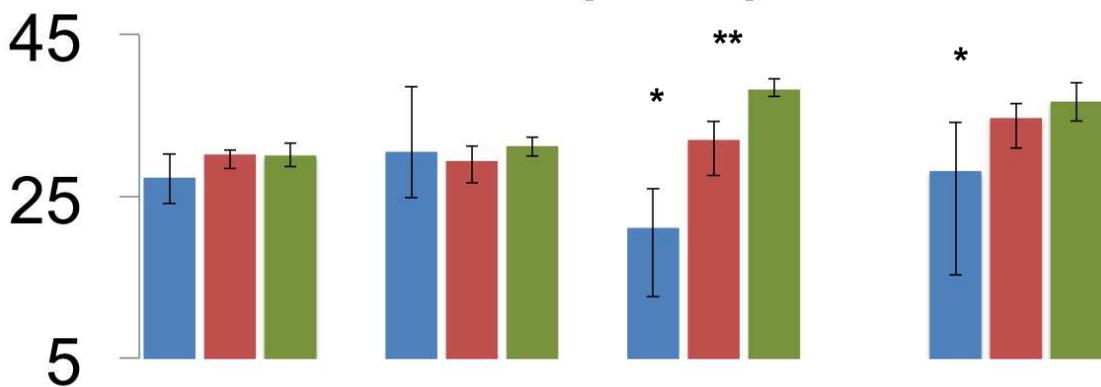
Locomotion speed (cm/s)
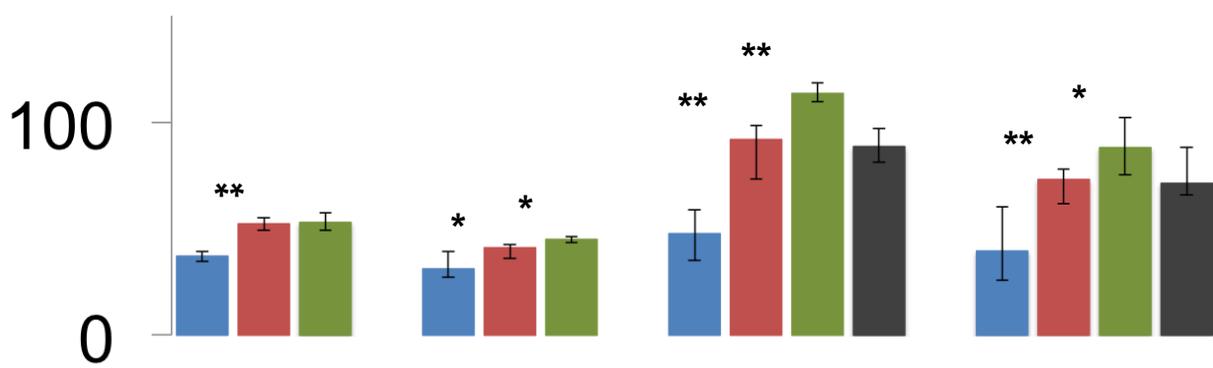
Set-point (º)
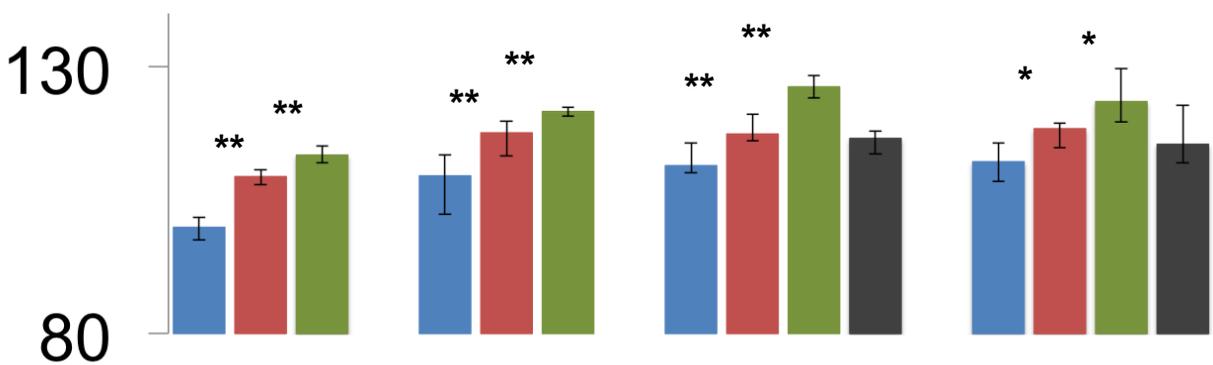
Frequency (Hz)
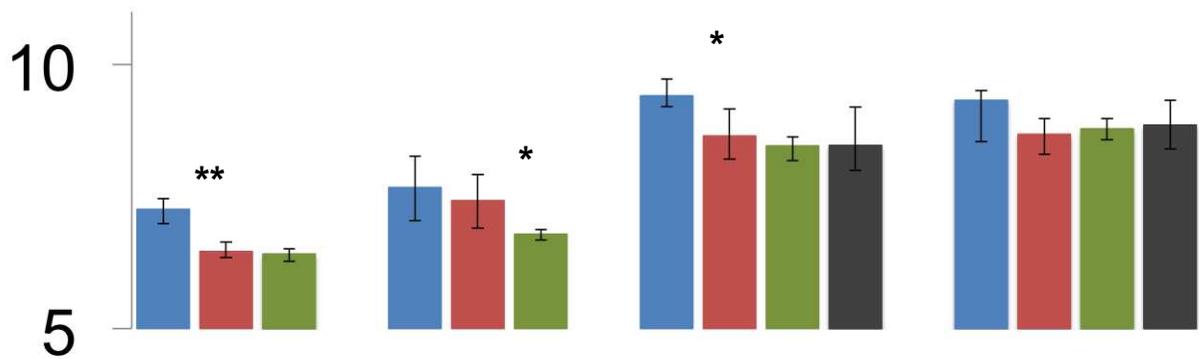
- Early
- Int.
- Late

Amplitude (º)
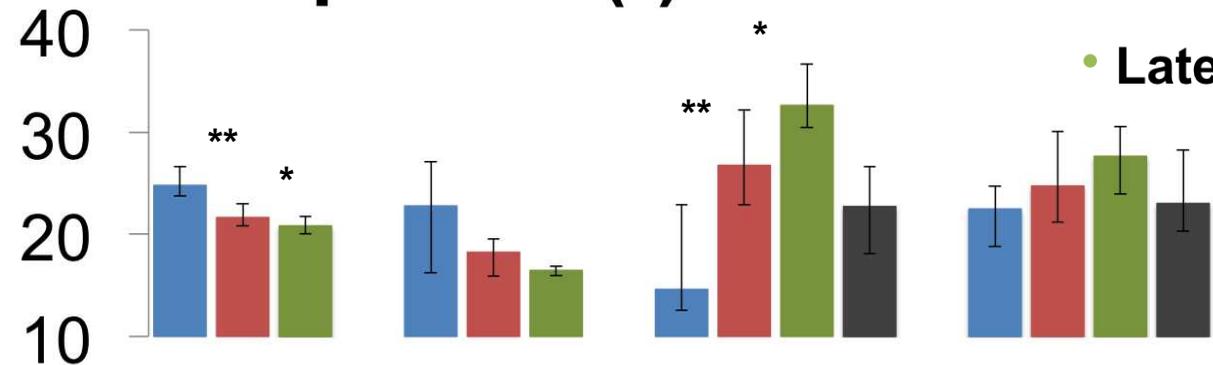
Condition

Figure 3

Set-point (º)

Unsighted
Sighted

Locomotion speed (cm/s)

No obstacles   Obstacles

Figure 4
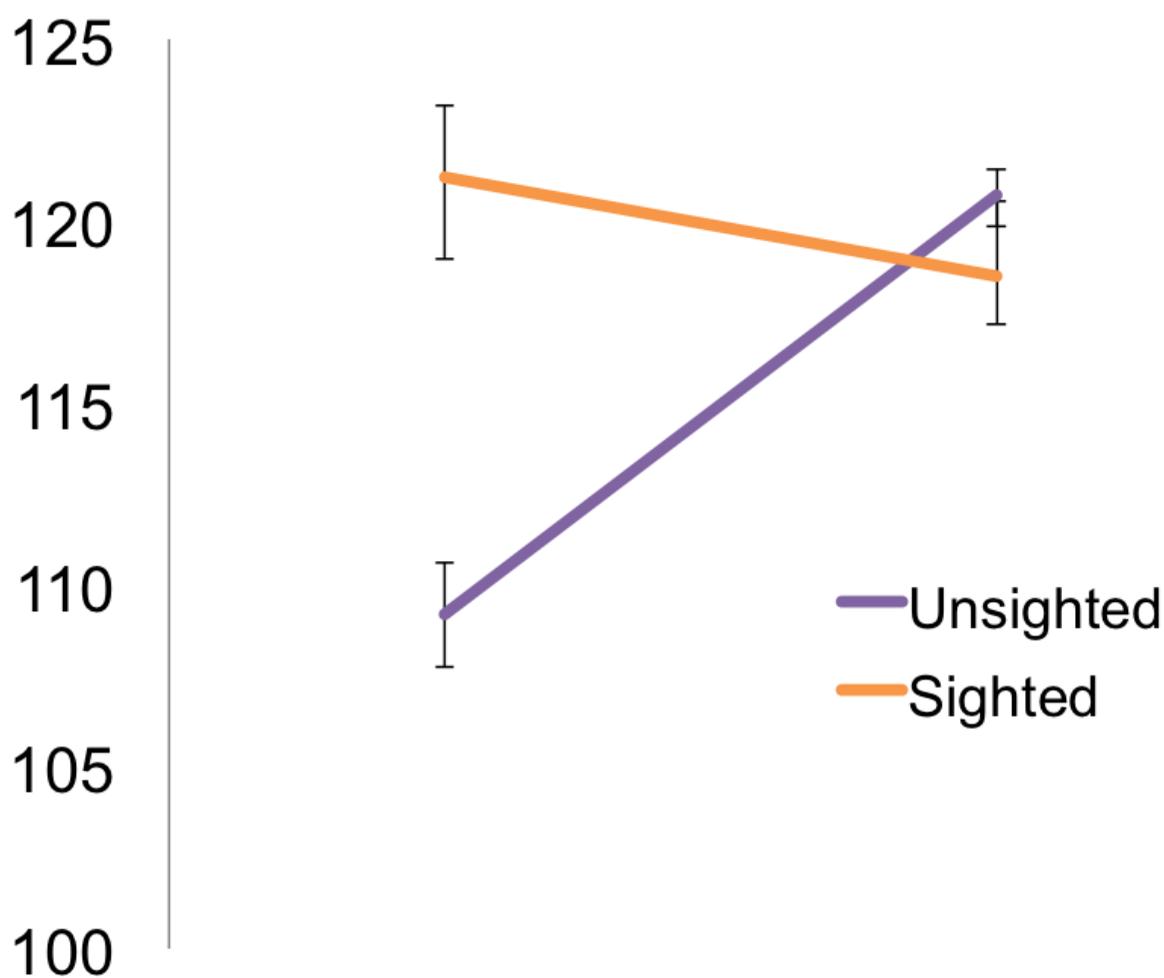
- 62 ms (before contact)   0 ms (contact)   + 48 ms   + 62 ms
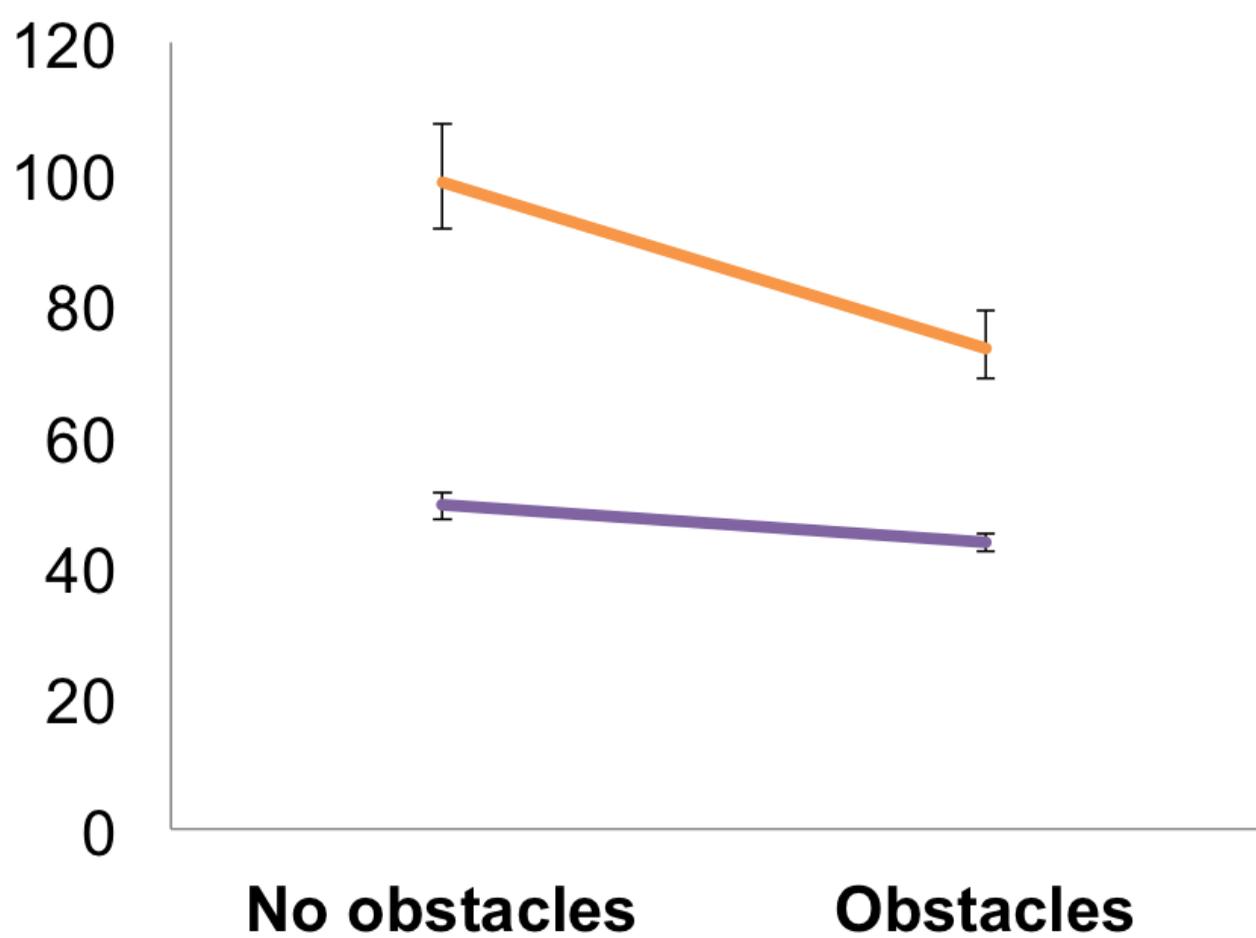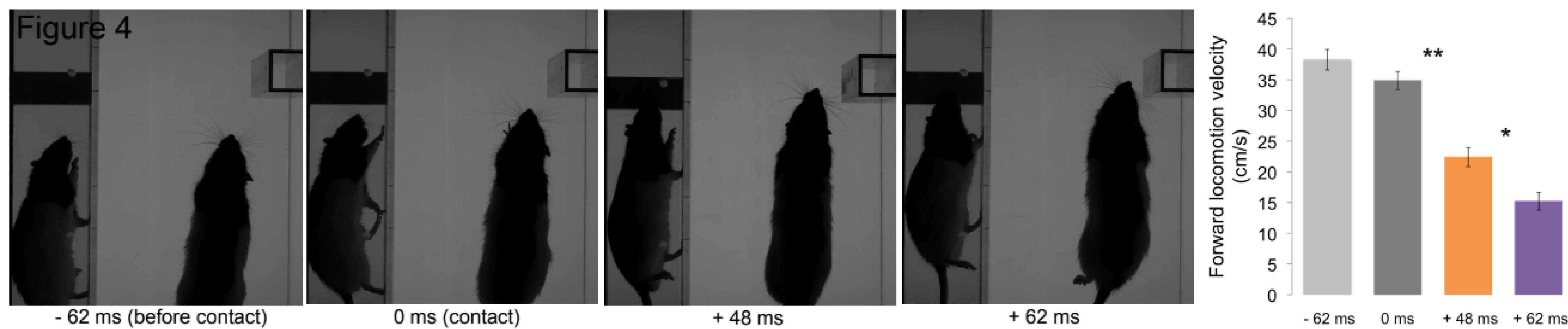
Supplemental Data
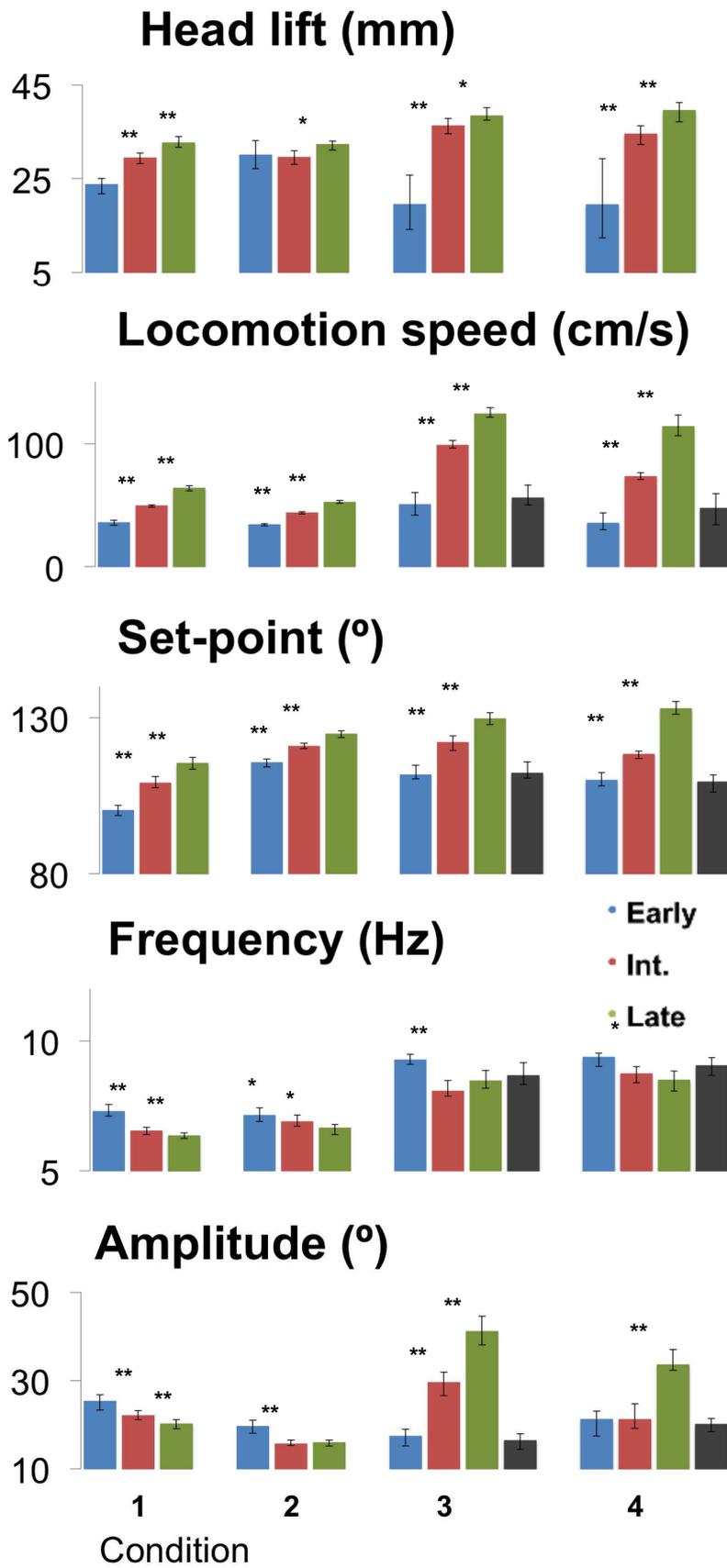
Figure S1, associated with main Figure 2. Histograms showing the effect of locomotion speed category – slow (blue), medium (red), and fast (green) – on mean locomotion and whisking variables from conditions 1–4: unsighted/no obstacles, unsighted/obstacles, sighted/no obstacles, sighted/obstacles. Grey-scale bars represent the first day of further training in dark environment (conditions 3 and 4 only). High-speed video clips were organized into slow, medium and fast locomotion speed categories by ranking all clips from each condition and assigning the slowest 33% to the slow category, the middle 33% to the medium category, and the fastest 33% to the fast category in order to obtain the same number of high-speed clips per category. As can be seen, patterns of locomotion and whisking behaviour are comparable to those found when assigning high-speed clips to the early, intermediate and late training stages (see main Figure 2). A Kruskal-Wallis ANOVA was used to examine the overall effect of training stage and follow-up Mann-Whitney U tests with a Bonferroni adjustment (α = .025) to examine discrete differences. Stars denote significance (* p < .025, ** p < .001). Medians are displayed, error bars show 95% confidence intervals.
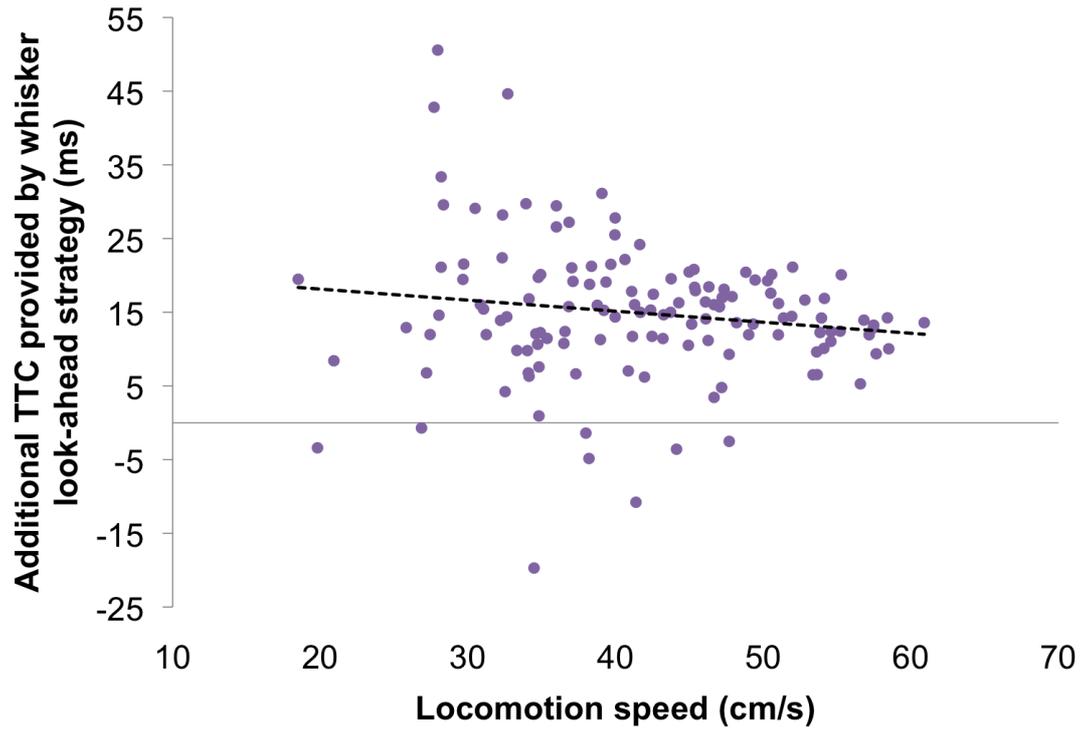
Figure S2, associated with main Figure 4. Look-ahead whisker strategy provides the rat with additional time to collision. One data point is one high-speed video clip from condition 2 (unsighted/obstacles), and shows the extra time between whisker tip contact and snout collision with an obstacle by using a look-ahead whisker strategy when compared to an exploratory strategy alone. The mean exploratory TLD was subtracted from the look-ahead TLD achieved in each high-speed clip in condition 2. The extra TTC that the look-ahead strategy provides marginally decreases as locomotion speed increases ($r = .17$, $p = .048$).
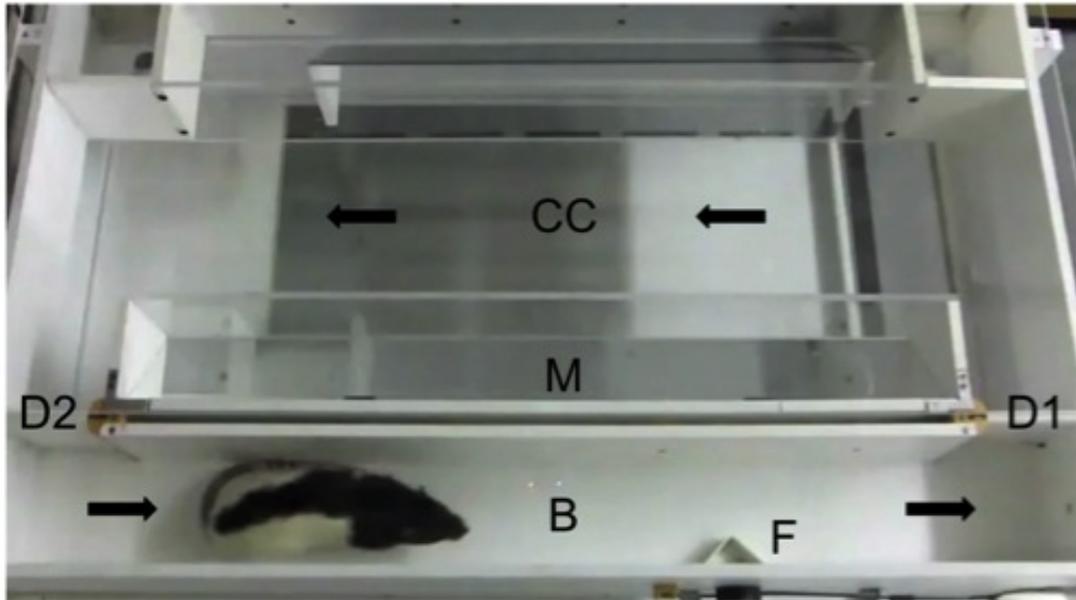
Figure S3, associated with Experimental Procedures. Purpose-built training arena used in all three experimental conditions. **CC**, central corridor; **B**, base arm; **F**, food hopper; **D1**, door 1; **D2**, door 2; **M**, side mirror. Arrows denote rat's direction of travel.
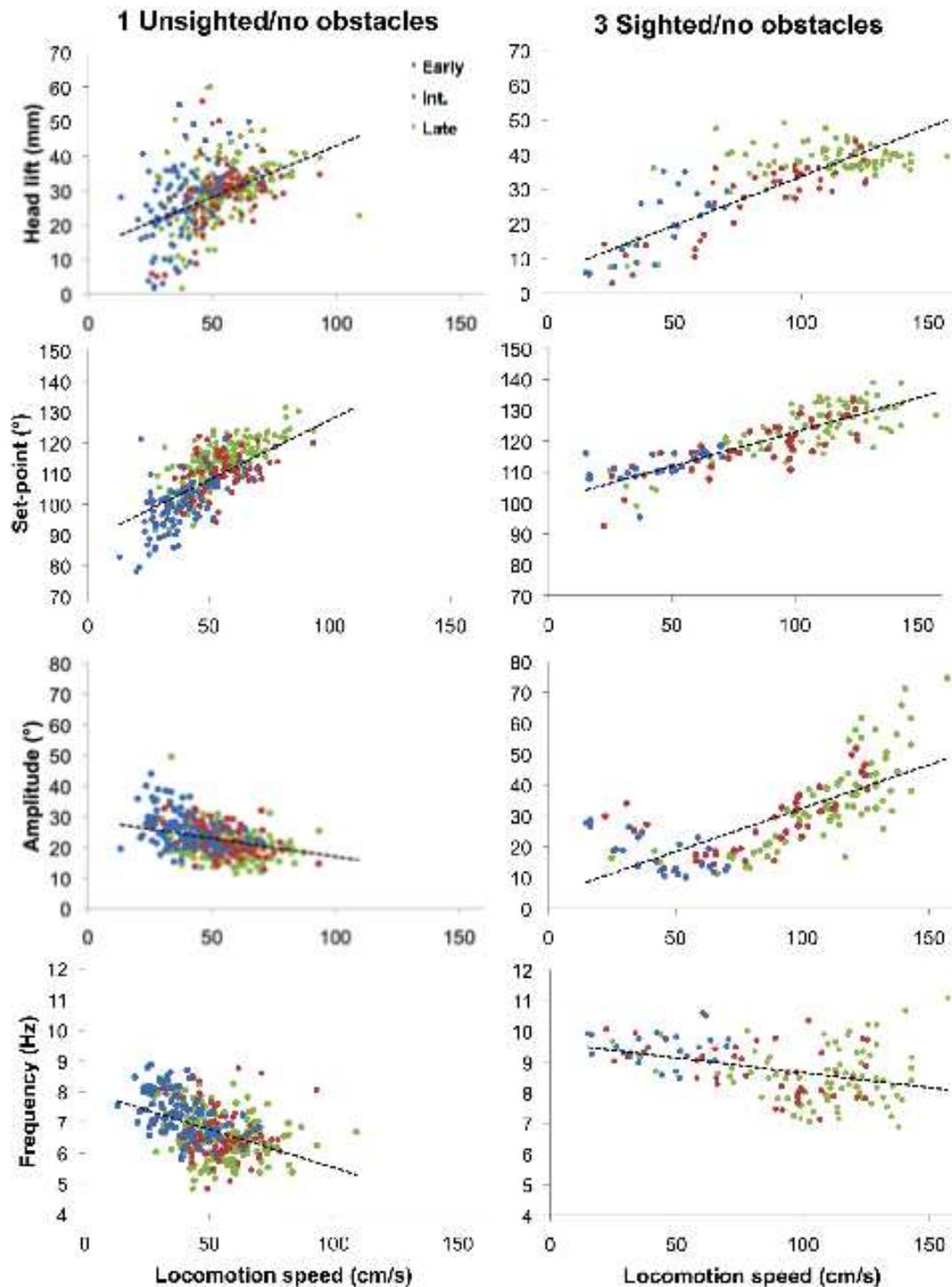
Figure S4, associated with main Results and Discussion. Scatterplots comparing partial correlations between locomotion speed, head lift and whisking kinematics for functionally-blind (condition 1, left column) and sighted animals (condition 3, right column) in environments without obstacles. Training stages overlaid (early, blue; intermediate, red; late, green). Each data point is one high-speed video clip. See also Table S2 for correlation coefficients.

Table S1, statistics associated with main Figure 2, main Figure 3 and Figure S1. Medians (95% confidence intervals) and detailed statistics. Nonparametric Kruskal-Wallis ANOVAs and Mann-Whitney *U* follow-up tests with Bonferroni adjustment (*p* < .025) compare the effect of training stage (main Figure 2) and speed category (Figure S1) on whisking and locomotion variables. Between-conditions comparisons with multivariate ANOVA and follow-up tests also shown. *NOTE*: Mann-Whitney *U* follow-up: [a] Early vs. Intermediate training stage *or* Slow vs. Medium speed category at *p* < .025; [b] Intermediate vs. Late training stage *or* Medium vs. Fast speed category at *p* < .025.

Training stage *Associated with main Figure 2*	Early	Intermediate	Late	3-Group comparisons
Condition 1 (unsighted / no obstacles)				
Locomotion speed	37.1 (34.6, 39.5)	52.3 (49.3, 55.0)	53.0 (49.3, 57.6)	H(2) = 92.52, *p* < .001[a]
Head lift	27.2 (24.1, 30.2)	30.1 (28.5, 30.8)	30.0 (28.7, 31.6)	H(2) = 6.82, *p* < .05
Set-point	99.9 (97.5, 101.86)	109.4 (107.8, 110.8)	113.4 (112.0, 115.2)	H(2) = 121.11, *p* < .001[a,b]
Amplitude	24.8 (23.7, 26.6)	21.6 (20.8, 23.0)	20.8 (20.1, 21.8)	H(2) = 49.30, *p* < .001[a,b]
Frequency	7.3 (7.0, 7.5)	6.5 (6.3, 6.6)	6.4 (6.3, 6.5)	H(2) = 62.82, *p* < .01[a]
Condition 2 (unsighted / obstacles)				
Locomotion speed	31.1 (27.2, 39.2)	41.1 (36.0, 42.6)	45.0 (43.3, 46.3)	H(2) = 24.62, *p* < .001[a,b]
Head lift	30.4 (24.8, 38.5)	29.3 (26.7, 31.3)	31.1 (30.0, 32.3)	H(2) = 1.72, *p* = .423
Set-point	109.5 (102.4, 113.5)	117.6 (113.2, 119.9)	121.6 (120.7, 122.4)	H(2) = 56.19, *p* < .001[a,b]
Amplitude	22.8 (16.2, 27.2)	18.3 (15.9, 19.6)	16.5 (16.0, 16.9)	H(2) = 10.84, *p* < .01
Frequency	7.7 (7.0, 8.3)	7.4 (6.9, 7.9)	6.8 (6.7, 6.9)	H(2) = 26.00, *p* < .001[b]
Condition 3 (sighted / no obstacles)				
Locomotion speed	47.7 (35.1, 58.9)	91.9 (73.3, 98.6)	113.5 (109.6, 118.3)	H(2) = 60.25, *p* < .001[a,b]
Head lift	21.0 (12.6, 26.0)	31.9 (27.6, 34.3)	38.1 (37.4, 39.5)	H(2) = 70.48, *p* < .001[a,b]
Set-point	111.5 (110.1, 115.6)	117.4 (116.1, 121.1)	126.1 (124.2, 128.4)	H(2) = 54.67, *p* < .001[a,b]
Amplitude	14.6 (12.5, 22.9)	26.8 (22.9, 32.2)	32.6 (30.5, 36.7)	H(2) = 36.88, *p* < .001[a,b]
Frequency	9.4 (9.2, 9.7)	8.6 (8.2, 9.2)	8.5 (8.2, 8.6)	H(2) = 22.08, *p* < .001[a]
In dark environment Days 1–3				
Locomotion speed	88.6 (81.1, 97.0)	85.9 (66.3, 103.5)	96.6 (83.2, 112.5)	H(2) = 5.90, *p* = .052[b]
Set-point	116.6 (114.0, 117.9)	119.1 (116.3, 120.6)	120.5 (116.8, 125.5)	H(2) = 8.63, *p* < .05[b]
Amplitude	22.7 (18.1, 26.6)	20.5 (17.6, 27.1)	27.1 (22.7, 31.5)	H(2) = 3.94, *p* = .139[b]
Frequency	8.5 (8.0, 9.2)	8.9 (8.4, 9.6)	9.2 (8.9, 9.5)	H(2) = 8.57, *p* < .05
Condition 4 (sighted / obstacles)				
Locomotion speed	39.5 (25.7, 60.4)	73.1 (61.7, 78.0)	88.1 (75.3, 102.2)	H(2) = 32.98, *p* < .001[a,b]
Head lift	28.0 (15.3, 34.1)	34.6 (30.9, 36.4)	36.6 (34.3, 39.1)	H(2) = 20.84, *p* < .001[a]
Set-point	112.2 (108.5, 115.7)	118.4 (114.8, 119.3)	123.4 (119.7, 129.7)	H(2) = 33.11, *p* < .001[a,b]
Amplitude	22.5 (18.1, 26.6)	24.7 (21.2, 30.1)	27.7 (23.9, 30.5)	H(2) = 4.46, *p* = .108
Frequency	9.3 (8.5, 9.5)	8.7 (8.3, 9.0)	8.8 (8.6, 9.0)	H(2) = 2.10, *p* = .350
In dark environment Days 1–3				
Locomotion speed	71.3 (65.8, 88.3)	72.4 (63.4, 82.2)	91.5 (79.0, 101.1)	H(2) = 5.41, *p* = .067
Set-point	115.5 (111.9, 122.7)	114.2 (110.8, 118.8)	121.1 (117.0, 122.9)	H(2) = 4.76, *p* = .092
Amplitude	23.0 (20.3, 28.2)	25.2 (21.5, 27.6)	30.4 (26.9, 36.1)	H(2) = 9.04, *p* < .05
Frequency	8.9 (8.4, 9.3)	8.5 (8.1, 8.8)	9.2 (8.4, 9.3)	H(2) = 5.02, *p* = .081

Speed category				
Associated with Figure S1	**Slow**	**Medium**	**Fast**	**3-Group comparisons**

Condition 1 (unsighted / no obstacles)

	Slow	Medium	Fast	3-Group comparisons
Locomotion speed	35.8 (33.5, 37.7)	49.5 (48.2, 50.4)	63.8 (61.6, 65.7)	H(2) = 313.78, $p < .001^{a,b}$
Head lift	23.8 (21.8, 25.0)	29.4 (28.2, 30.5)	32.6 (31.6, 34.0)	H(2) = 76.96, $p < .001^{a,b}$
Set-point	100.3 (98.7, 101.9)	109.1 (107.6, 111.2)	115.4 (113.5, 117.3)	H(2) = 176.55, $p < .001^{a,b}$
Amplitude	25.3 (23.3, 26.8)	22.1 (21.1, 23.2)	20.2 (19.1, 21.1)	H(2) = 55.04, $p < .001^{a,b}$
Frequency	7.3 (7.1, 7.6)	6.5 (6.4, 6.7)	6.4 (6.2, 6.5)	H(2) = 72.07, $p < .001^{a}$

Condition 2 (unsighted / obstacles)

	Slow	Medium	Fast	3-Group comparisons
Locomotion speed	34.1 (33.1, 34.9)	43.7 (42.8, 44.6)	52.4 (51.4, 53.8)	H(2) = 290.67, $p < .001^{a,b}$
Head lift	30.1 (27.2, 33.2)	29.6 (28.0, 31.0)	32.3 (31.1, 33.0)	H(2) = 4.84, $p = .089^{b}$
Set-point	115.6 (114.2, 116.7)	120.9 (120.1, 121.8)	124.8 (123.7, 125.8)	H(2) = 150.10, $p < .001^{a,b}$
Amplitude	19.6 (18.1, 21.0)	15.7 (15.3, 16.6)	16.0 (15.2, 16.6)	H(2) = 46.12, $p < .001^{a}$
Frequency	7.1 (6.9, 7.4)	6.9 (6.7, 7.2)	6.7 (6.4, 6.8)	H(2) = 26.85, $p < .001^{a,b}$

Condition 3 (sighted / no obstacles)

	Slow	Medium	Fast	3-Group comparisons
Locomotion speed	50.5 (41.8, 60.3)	98.7 (96.4, 102.5)	124.1 (121.3, 129.0)	H(2) = 132.45, $p < .001^{a,b}$
Head lift	19.5 (14.1, 25.7)	36.3 (34.6, 37.8)	38.4 (37.5, 40.1)	H(2) = 76.32, $p < .001^{a,b}$
Set-point	111.7 (110.4, 114.9)	122.1 (119.5, 124.3)	129.7 (127.8, 131.6)	H(2) = 101.06, $p < .001^{a,b}$
Amplitude	17.4 (15.2, 19.0)	29.6 (26.6, 31.9)	41.1 (38.1, 44.6)	H(2) = 94.29, $p < .001^{a,b}$
Frequency	9.3 (9.1, 9.5)	8.1 (7.9, 8.5)	8.5 (8.2, 8.9)	H(2) = 36.12, $p < .001^{a}$

In dark environment

	Slow	Medium	Fast	3-Group comparisons
Locomotion speed	55.9 (50.1, 66.3)	91.1 (86.4, 94.4)	120.4 (111.4, 126.4)	H(2) = 104.89, $p < .001^{a,b}$
Set-point	112.2 (110.7, 115.9)	118.9 (116.8, 121.9)	122.1 (119.6, 126.7)	H(2) = 43.10, $p < .001^{a,b}$
Amplitude	16.4 (14.4, 18.0)	23.1 (19.9, 26.7)	33.3 (30.6, 38.0)	H(2) = 60.28, $p < .001^{a,b}$
Frequency	8.7 (8.3, 9.2)	8.8 (8.4, 9.4)	9.6 (8.8, 9.8)	H(2) = 11.56, $p < .01^{b}$

Condition 4 (sighted / obstacles)

	Slow	Medium	Fast	3-Group comparisons
Locomotion speed	35.3 (30.1, 43.9)	73.2 (70.7, 76.4)	113.9 (106.4, 123.1)	H(2) = 139.56, $p < .001^{a,b}$
Head lift	19.5 (12.4, 29.3)	34.5 (32.3, 36.3)	39.6 (37.1, 41.2)	H(2) = 60.00, $p < .001^{a,b}$
Set-point	110.0 (108.2, 112.5)	118.3 (117.0, 119.2)	132.9 (131.1, 135.2)	H(2) = 122.12, $p < .001^{a,b}$
Amplitude	21.2 (17.4, 23.0)	21.2 (19.2, 24.7)	33.6 (32.4, 37.1)	H(2) = 78.39, $p < .001^{b}$
Frequency	9.4 (9.0, 9.5)	8.7 (8.4, 9.0)	8.5 (8.1, 8.8)	H(2) = 19.51, $p < .001^{a}$

In dark environment

	Slow	Medium	Fast	3-Group comparisons
Locomotion speed	47.5 (34.1, 59.2)	79.5 (73.3, 82.3)	113.8 (103.3, 118.6)	H(2) = 99.56, $p < .001^{a,b}$
Set-point	109.4 (106.2, 111.7)	118.0 (114.5, 120.5)	126.8 (123.4, 129.9)	H(2) = 63.46, $p < .001^{a,b}$
Amplitude	20.1 (18.4, 21.5)	26.3 (24.4, 28.8)	39.2 (35.4, 45.6)	H(2) = 66.54, $p < .001^{a,b}$
Frequency	9.1 (8.7, 9.4)	8.4 (7.8, 9.0)	8.6 (8.2, 9.2)	H(2) = 7.39, $p < .025^{a}$

Multivariate ANOVA

Associated with main Figure 3

	Main effects		
	Visual cues	**Collision risk**	**Interactions**
	$F(5,982) = 519.19$, $p < .001$	$F(5,982) = 44.15$, $p < .001$	$F(5,982) = 11.56$, $p < .001$
Follow-up univariate tests			
Locomotion speed	$F(1,986) = 617.926$, $p < .001$	$F(1,986) = 51.60$, $p < .001$	$F(1,986) = 7.772$, $p < .01$
Head lift	$F(1,986) = 9.40$, $p < .01$	$F(1,986) = 2.52$, $p = .113$	$F(1,986) = 2.89$, $p = .089$
Set-point	$F(1,986) = 81.07$, $p < .001$	$F(1,986) = 34.23$, $p < .001$	$F(1,986) = 46.36$, $p < .001$
Amplitude	$F(1,986) = 222.54$, $p < .001$	$F(1,986) = 61.28$, $p < .001$	$F(1,986) = 2.85$ $p = .092$
Frequency	$F(1,986) = 778.07$, $p < .001$	$F(1,986) = 5.46$, $p < .05$	$F(1,986) = .631$, $p = .427$

Table S2, associated with Figure S4. Partial bootstrapped Pearson's correlations between locomotion speed and whisking kinematics and head lift. Partial correlation coefficient (controlling for all other variables), 95% confidence intervals and significance levels shown.

Locomotion speed correlated with…	Condition 1 (unsighted / no obstacles)	Condition 2 (unsighted / obstacles)	Condition 3 (sighted / no obstacles)	Condition 3 *In the dark*	Condition 4 (sighted / obstacles)	Condition 4 *In the dark*
Head lift	.435 (95% CI: .34, .52) $p < .001$	.115 (95% CI: −.02, .25) $p < .05$	.807 (95% CI: .74, .86) $p < .001$	Not available	.647 (95% CI: .54, .73) $p < .001$	Not available
Set-point	.658 (95% CI: .59, .72) $p < .001$	.710 (95% CI: .64, .77) $p < .001$	.884 (95% CI: .86, .91) $p < .001$	.692 (95% CI: .58, .77) $p < .001$	..907 (95% CI: .88, .93) $p < .001$	.831 (95% CI: .77, .88) $p < .001$
Amplitude	−.293 (95% CI: −.20, −.39) $p < .001$	−.472 (95% CI: −.36, −.57) $p < .001$	.712 (95% CI: .64, .78) $p < .001$	.707 (95% CI: .60, .79) $p < .001$	.564 (95% CI: .45, .66) $p < .001$	.687 (95% CI: .60, .77) $p < .001$
Frequency	−.330 (95% CI: −.23, −.42) $p < .001$	−.239 (95% CI: −.14, −.35) $p < .001$	−.358 (95% CI: −.52, −.19) $p < .001$	.168 (95% CI: .01, .33) $p = .070$	−.278 (95% CI: −.43, −.12) $p < .001$	−.128 (95% CI: −.28, .01) $p = .181$

Supplemental Experimental Procedures

Here we describe details of our methods that were not provided in the main report.

Animals

The presented study was conducted at the Active Touch Laboratory at the University of Sheffield (ATL@S), UK. The experimental animals were dystrophic (functionally-blind) Royal College of Surgeons (RCS) rats (used in conditions 1 and 2) and sighted Hooded Lister (HL) rats (used in conditions 3 and 4). Dystrophic RCS animals have a specific mutation that causes a gradual degeneration of the retina, with consequent near complete loss of vision in the mature animal [S1]; vibrissal tactile sensing is unimpaired [S2-S3], hence these animals provide an effective control for use of vision in experiments on vibrissal touch [S2-S6]. In condition 1 (unsighted/no obstacles), seven male RCS rats were used, and at the time of the experiment were aged 8-11 months and weighed 300-400 grams. For condition 2 (unsighted/obstacles), three male RCS rats aged nine months old and weighing between 300-400 grams were used. For condition 3 (sighted/no obstacles), four male HL rats were used, and for condition 4 (sighted/obstacles), five male HL rats were used, all aged 2-3 months and weighing 250-350 grams. All animals were kept in a 12:12 light/dark schedule and maintained at 22ºC. One week prior to the experimental period, animals were handled daily and served a restricted diet, but maintained to within 90% of their baseline body weight, in order to motivate them to run the arena for food reward. All procedures were approved by the UK Home Office, under the terms of the UK Animals (Scientific Procedures) Act, 1986.

Experimental setup

High-speed videography was used to record the whisking and locomotion behavior of rats trained to run circuits of an arena for food reward. Animals were filmed using a Photron Fastcam PCI camera, recording at 500 frames/s, shutter speed of 0.5ms, and resolution of 1024 x 1024 using a 50 mm lens. The camera was suspended from the ceiling to obtain an overhead view of the rat whilst in motion along the central corridor (CC, 193 x 680 mm, e.g. see main Figure 1) of a purpose-built training arena (see Figure S3). A front-silvered mirror (M) in view of the overhead high-speed camera, positioned alongside the central corridor and angled at approximately 45°, allowed a simultaneous side view of the locomoting animal to be obtained. The clear Perspex floor and ceiling allowed illumination from a custom-built high-power light box (with the exception of conditions 3 and 4 whereby animals also locomoted in a darkened arena under illumination from an infrared light box), positioned beneath the arena, providing a clear silhouette of the whiskers and body in the overhead view, and in the side view by means of an angled front-silvered mirror (see, e.g. main Figure 1; with the exception that the side view could not be viewed in conditions 3 and 4 in the dark environment owing to limitations of the infrared light box). The training arena contained animal location sensors (beam breaks) that allowed the automatic control of a food hopper and two doors (D1, D2) linking the central corridor to the narrower base corridor (B). This setup allowed the animal's direction of travel to be constrained to anti-clockwise circuits as described below. A calibration tool of known size and dimensions was filmed at the start of each experimental session in order to translate pixel data from the video clips into units of length (mm).

Experimental procedures

All conditions required the animal to locomote down the central corridor of the training arena. In condition 1 (unsighted/no obstacles condition), and condition 3 (sighted/no obstacles condition) the rat was first placed into the base corridor, after which the experiment was started and the first door opened. Once the animal had entered the central

corridor and triggered a beam break halfway along, the first door closed and the second, at the opposite end of the central corridor, opened, allowing the animal to proceed anti-clockwise into the far end of the base corridor where a 50mg food pellet reward was provided. When the animal reached the food hopper, a further beam break was triggered, signaling the closure of the second door and the reopening of the first, thus beginning the next experimental cycle. Each daily experimental session lasted either 30 minutes, or was halted after the rat had completed 40 cycles; the learning criteria for the experiment, and threshold for inclusion in the analysis, was three consecutive sessions of 40 cycles. In each session, a high-speed video clip of 1.6 seconds was recorded in every second cycle, using a manual trigger, until 12 clips in total had been recorded. Each animal completed one experimental session per day, Monday to Friday, and the pellets of food consumed whilst in the training arena were subtracted from its daily dietary allowance. The animal received food *ad libitum* at the weekend. All animals took part in the experiment for at least five sessions, but as individuals differed in the speed at which they reached the learning criterium, this was extended, where needed, until the requirement for three consecutive days of 40 cycles was met.

For condition 2 (unsighted/obstacles) and condition 4 (sighted/obstacles), the experimental setup and procedures described above were modified in order to explore the impact of a changing environment on locomotion and whisking behavior. Metal cuboid objects (50 x 50 mm x 100 mm; L x W x H) were placed into the central corridor as obstacles. During experimental sessions, one obstacle was always present in one of four locations in the central corridor—two locations along the left-hand wall and the other two along the right-hand wall (see main Figure 4 and Movie S2). After every fifth cycle, the obstacle was manually moved to a predetermined randomly assigned location whilst the animal waited in the side corridor.

Sighted animals in conditions 3 and 4 also moved along the corridor in darkness for

three consecutive days following previous training in the lit environment. High-speed video clips were obtained using illumination from an infrared light box.

Data selection

In all conditions, all video clips, or sections thereof, depicting a minimum of three whisks, during which the animal moved along central corridor with the entire whisker field in view, were examined for potential inclusion in the analysis. Clips were subsequently excluded if the rat could be seen to be following either wall with its whiskers, was stationary, was orienting to a specific part of the arena, making head turns, or showed pitch, roll or yaw of the head greater than approximately 45º. Clips showing whisker contacts with walls (wall-following), immobility, or orienting were removed since the focus of investigation was to understand unimpeded locomotion; those showing head turns, pitch, roll and yaw were removed since it becomes difficult to track the location of the whiskers when the head position departs markedly from a plane parallel to that of the overhead camera view, and head turning is known to be accompanied by changes in whisk strategy [S7]. In conditions 2 and 4 (obstacles) we additionally excluded clips (or portions thereof) in which the rat made whisker contacts with the obstacle – therefore this data could include occasions before or after obstacle contact. For an overview of the total amount of high-speed video data collected and analyzed per condition and animal, see the following Table.

Exclusion	Number of high-speed clips
Condition 1 (unsighted/no obstacles)	
	Recorded – 531
Already fulfilled 'late-training' requirements	152
Head turns and head pitch, roll and yaw	14
Whisker contacts with walls	10
Stationary (not locomoting)	1
Poor tracking	0
	Included in analysis – 354
Animals (N = 7)	
1.1	42
1.2	46
1.3	51
1.4	43
1.5	68
1.6	51
1.7	53
Condition 2 (unsighted/obstacles)	
	Recorded – 606
Already fulfilled 'late-training' requirements	0
Head turns and head pitch, roll and yaw	27
Whisker contacts with walls	24
Stationary (not locomoting)	8
Obstacle contact only (no locomotion)	218
Poor tracking	5
	Included in analysis – 324
Animals (N = 3)	
2.1	93
2.2	95
2.3	136
Condition 3 (sighted/no obstacles)	
	Recorded – 226
Already fulfilled 'late-training' requirements	48
Head turns and head pitch, roll and yaw	8
Whisker contacts with walls	15
Stationary (not locomoting)	5

Poor tracking	0
	Included in analysis – 150

Animals (N = 4)

3.1	43
3.2	34
3.3	38
3.4	35
In dark environment	Recorded – 144
Head turns and head pitch, roll and yaw	19
Whisker contacts with walls	3
Stationary (not locomoting)	3
Poor tracking	0
	Included in analysis – 119

Animals

3.1	30
3.2	33
3.3	34
3.4	22

Condition 4 (sighted/obstacles)

	Recorded – 307
Already fulfilled 'late-training' requirements	60
Head turns and head pitch, roll and yaw	25
Whisker contacts with walls	9
Obstacle contact only (no locomotion)	50
Stationary (not locomoting)	5
Poor tracking	0
	Included in analysis – 158

Animals (N = 5)

4.1	19
4.2	29
4.3	37
4.4	29
4.5	44

In dark environment	Recorded – 178
Head turns and head pitch, roll and yaw	34
Whisker contacts with walls	4
Obstacle contact only (no locomotion)	18
Stationary (no locomotion)	9
Poor tracking	0
	Included in analysis – 113

Animals

4.1	18
4.2	25
4.3	30
4.4	20
4.5	20

Time-to-collision analysis (data from condition 2)

Randomly selected from the 324 selected clips from condition 2	
	Included in analysis – 133

Animals (*N* = 3)

2.1	39
2.2	35
2.3	59

Deceleration rate analysis (data from condition 2)

	Clips showing obstacles contacts – 367
Head turns (before whisker contact) and head pitch, roll and yaw	24
Whisker contacts with walls	47
No approach to obstacle/first whisker contact unseen or not clear	132
No orient to obstacle	164
	Included in analysis – 57

Animals (*N* = 3)

2.1	23
2.2	12
2.3	21

Whisker and snout tracking

In all conditions, the animal's whiskers and snout were tracked in the overhead view, and its snout in the side view, using the BIOTACT Whisker Tracking Tool (BWTT) [S8], which allows semi-automatic detection, and tracking of the contours of the whiskers and head. From this method, as described in [S8] 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 ('snout data'), and of a set of estimated whisker base angles ('whisker data') indicating whisker angular positions relative to the midline of the snout. Data from all conditions were processed identically, with the exception that the side view in conditions 2 and 4 sometimes had fewer frames available (compared to the overhead view) due to the obstacle occluding the view of the rat in the side mirror (see main Figure 4 for an example). Additionally, there was no side view of animals (and therefore no measure of head lift) in conditions 3 and 4 in the dark environment due to limitations of our infrared light box. The accuracy of automatic tracking was judged by manual review and visual inspection. Video clips were discarded unless the visible whiskers had been correctly identified in the tracking results in the great majority of video frames.

Whisking and locomotion variables

To give an accurate description of periodic whisker movement, the variables we chose to calculate, for each analyzed clip, were the whisker *set-point*, *amplitude* and *frequency* (for an overview of all analyzed variables see the table below). Specifically, using the tracked whisker data, we computed the mean angle of the whiskers on each side of the snout calculated as the average value of the measured angular positions of all identified whiskers on each side. These time series, denoted as θ_L and θ_R, can be recovered for each video clip from the automatic tracking results (see, e.g. main Figure 1, right hand column) and has been shown to provide a reliable estimate of the overall position of the tracked whisker field [S6]. For each of the time series θ_L and θ_R, we computed the set-

point, amplitude and frequency as follows. Whisker *set-point* was calculated for the entire clip by taking the mean across all tracked frames, and the *amplitude* by taking the root mean square (RMS) across all tracked frames. To calculate whisk *frequency*, a measure of whisk *power* was first calculated by taking the average power spectral density (PSD) of the θ_L and θ_R across the clip within the range of 4-12 Hz [S6 S9] using the Fourier transform, before taking the centre of mass (CoM; average frequency weighted by power) of these computed PSDs. To obtain a single summary value for each trial from these bilateral quantities, we took the mean across the two sides; it is these per-trial summary values that are presented in the main report.

Locomotion variables were calculated using the tracked snout data, again averaging across each entire clip, focusing on *locomotion speed* (cm/s) and *head lift* (mm) relative to the floor. *Locomotion speed* was calculated using the time and distance traveled by the rat's snout tip and *head lift* from the floor by tracking the snout in the side view using the BWTT and the position of the floor using a purpose built manual tracker (as used in [S5]). Initial measurements were in pixel data, and were subsequently transformed into units of length (mm) using information from the calibration tool. Bellow follows a summary table of whisker and locomotion variables calculated. We calculated the whisker variables for each of the time series, θ_L (left whisker field) and θ_R (right whisker field) and took the mean across the two sides to obtain a single summary value for each high-speed video clip from these bilateral quantities; it is these per-trial summary values that are presented in the main report.

Variable	Unit	Description
Whisker variables		
Mean whisker set-point	degrees	Average angular position of the whiskers (higher values denote more protracted whiskers)
Mean whisk amplitude	degrees	Average angular amplitude of the movement of the whiskers, found by taking the per-trial root-mean-square (RMS) of the whisker movements (higher values denote larger back and forth sweeps of the whiskers)
Mean whisk frequency	Hz	Average number of periodic variations (whisks) in the mean angle of the whiskers per second
Tactile look-ahead distance (TLD)	(mm)	Average distance between the point of the most rostral whisker tip and snout tip position
Exploratory TLD		The mean TLD found for eight high-speed video clips from the early training stage of condition 1 (no obstacles/unsighted)
Look-ahead TLD		The TLD for each high-speed clip in condition 2 (no obstacles)
Locomotion variables		
Mean locomotion speed	cm / s	Using the snout tip position, the distance travelled by the rat divided by the time taken to travel that distance (mean between forward and lateral movement)
Mean head lift	cm	Distance between the rat's snout tip position and the floor averaged across one high-speed clip
Mean time to collision (TTC)	ms	The time it would take between contact with the most rostral whisker tip, and subsequent collision with the snout tip if the rat maintained the same speed it is running at

Time-to-collision

Since we were interested in the possible role of the macrovibrissae in obstacle-avoidance we sought to estimate how much extra *time-to-collision* (TTC) was provided by an increase in whisker set-point, and furthermore how useful this amount of extra time may be in aiding deceleration. In order to investigate this we first calculated the an-

imal's *tactile look-ahead distance* (TLD) using a manual whisker tracking tool [S4]. Specifically, in every fourth video frame, the position of the snout tip and of the most rostral whisker tip was tracked in the overhead view using a horizontal rule perpendicular to the corridor (approximately the animal's direction of travel), and the distance between the two points measured. The mean distance between snout tip and whisker tip was then taken across each high-speed clip as a measure of TLD. To examine the effect of a change in attentional strategy on TLD required a baseline measure which we calculated as the mean TLD for eight clips showing typical exploratory whisking from the *early* training stage of condition 1 (unsighted/no obstacles). We then calculated the net *additional TLD* provided by any relative change in whisker set-point, for each high-speed video clip in condition 2 (unsighted/obstacles) by subtracting the baseline exploratory TLD from the average TLD for that clip. The additional time-to-collision was then calculated for each condition 2 clip by dividing the estimated additional TLD by locomotion speed in that clip.

Increasing TTC provides the animal with additional response time within which to decelerate in order to avoid, or reduce the impact of, collision with the obstacle. We therefore wished to estimate the rate of deceleration that animals can achieve following unexpected obstacle contacts. In order to do this, example high-speed video clips (or sections thereof), from condition 2, showing instances of whisker-obstacle contacts and subsequent deceleration of forward movement were selected and position of the snout tip tracked in the overhead view (using the manual tracking tool) in the period immediately proceeding and immediately following contact. Using this data, we measured 'instantaneous' forward locomotion velocity (cm/s) using the average movement of the position of the snout tip across three high-speed video frames (6 ms in total). In order to explore deceleration, we computed four 'instantaneous' forward locomotion velocities at -62 ms (pre-contact), 0 ms (contact), +48 ms and +62 ms (these times were chosen to reflect the time-to-collision estimates using exploratory and look-ahead whisker strategies) and used Kruskall-Wallis and follow-up Mann-Whitney U tests to uncover whether

significant deceleration had occurred between these four short (6 ms) periods of the whisker-obstacle contact event.

As discussed in the main manuscript, by increasing whisker set-point rats were able to provide themselves with an average *tactile look-ahead distance* (TLD; distance from snout-tip to whisker-tip) of 24.6 mm (SD = 3.7 mm) compared to 18.6 mm (SD = 0.3 mm) for an exploratory whisking strategy. Sighted animals from condition 4 (obstacles, 158 high-speed clips) also adopted an increased TLD of 23.8 mm (SD = 0.4 mm) compared to the exploratory whisking strategy of 15.3 mm (SD = 0.1 mm; means of seven clips from the early training stage of condition 3). However, due to much higher locomotion speeds, the TTC was lower than in unsighted animals (38 ms, SD = 20 ms and 38 ms, SD = 16 ms, using a look-ahead strategy and 53 ms, SD = 0.1 ms, using an exploratory strategy).

Statistical considerations

All reported statistics were calculated using nonparametric tests, with the exception of a multivariate ANOVA to investigate the interaction between the expectation of obstacles and the availability of visual cues, and Pearson's partial correlation tests that were performed using bootstrapping (1000 iterations). For tests with more than two independent groups the Kruskal-Wallis one-way ANOVA was used, and for follow-up *post hoc* tests (comparing two independent groups) the Mann-Whitney *U* test with a Bonferroni adjustment was chosen, along with their effect sizes [S10]. Nonparametric statistics are a robust method of statistical inference, even with datasets violating assumptions of normality [S11]. Similarly, bootstrapping correlation is a commonly used resampling method used for non-normally distributed data, and supports tests of partial correlations [S12]. Parametric analyses resulted in much the same result as their nonparametric equivalents.

Supplemental References

S1. McGill, T. J., Douglas, R. M., Lund, R. D., and Prusky, G. T. (2004). Quantification of spatial vision in the Royal College of Surgeons rat. Invest. Ophthalmol. Vis. Sci. 45, 932-936.

S2. Brecht, M., Preilowski, B. and Merzenich, M. M. (1997). Functional architecture of the mystacial vibrissae. Behav. Brain Res. 84, 81-97.

S3. Hetherington, L., Benn, M., Coffey, P. J., and Lund, R. D. (2000). Sensory capacity of the Royal College of Surgeons rat. Invest, Ophthalmol. Vis. Sci. 41, 3979-3983.

S4. Mitchinson, B., Martin, C. J., Grant, R. A. and Prescott, T. J. (2007). Feedback control in active sensing: Rat exploratory whisking is modulated by environmental contact. P. Roy. Soc. Lond. B Bio. 274, 1035-1041.

S5. Grant, R. A., Mitchinson, B., Fox, C. and Prescott, T. J. (2009). Active touch sensing in the rat: Anticipatory and regulatory control of whisker movements during surface exploration. J. Neurophysiol. 101, 862-874.

S6. Mitchinson, B., Grant, R. A., Arkley, K., Rankov, V., Perkon, I. and Prescott, T. J. (2011). Active vibrissal sensing in rodents and marsupials. Philos. Trans. Roy. Soc. B: Biol. Sci. 366, 3037-3048.

S7. Towal, R. B. and Hartmann, M. J. (2006). Right-left asymmetries in the whisking behavior of rats anticipate head movements. J. Neurosci. 26, 8838-8846.

S8. Perkon, I., Kosir, A., Itskov, P. M., Tasic, J., and Diamond, M. E. (2011). Unsupervised quantification of whisking and head movement in freely moving rodents. J. Neurophysiol. 105, 1950-1962.

S9. Berg, R. W. and Kleinfeld, D. (2003). Rhythmic whisking by rat: Retraction as well as protraction of the vibrissae is under active muscular control. J. Neurophysiol. 89, 104-117.

S10. Fritz, C. O., Morris, P. E., and Richler, J. J. (2012). Effect size estimates: current use, calculations, and interpretation. J. Exp. Psychol. 141, 2-18.

S11. Siegel, S. (1956). Nonparametric statistics for the behavioral sciences. New York: McGraw-Hill.

S12. SPSS Inc. (2009). PASW Bootstrapping 18. Chicago, Illinois: SPSS Inc.

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