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1 **Spatial navigation signals in rodent visual cortex**

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4 Tom Flossmann¹ and Nathalie L. Rochefort^{1,2,*}5 ¹Centre for Discovery Brain Sciences, School of Biomedical Sciences Edinburgh, Edinburgh, EH8 9XD,
6 United Kingdom.7 ²Simons Initiative for the Developing Brain, University of Edinburgh, Edinburgh, EH8 9XD, United
8 Kingdom.

9 *Corresponding Author:

10 Nathalie Rochefort

11 Centre for Discovery Brain Sciences,

12 Biomedical Sciences Edinburgh,

13 Edinburgh, EH8 9XD, United Kingdom.

14 n.rochefort@ed.ac.uk

15

16

17 **Abstract**

18 During navigation, animals integrate sensory information with body movements to guide actions.
19 The impact of both navigational and movement-related signals on cortical visual information
20 processing remains largely unknown. We review recent studies in awake rodents that have revealed
21 navigation-related signals in the primary visual cortex (V1), including speed, distance travelled and
22 head-orienting movements. Both cortical and subcortical inputs convey self-motion related
23 information to V1 neurons: for example, top-down inputs from secondary motor and retrosplenial
24 cortices convey information about head movements and spatial expectations. Within V1, subtypes of
25 inhibitory neurons are critical for the integration of navigation-related and visual signals. We
26 conclude with potential functional roles of navigation-related signals in V1 including gain control,
27 motor error signals and predictive coding.

28

29 **Introduction**

30 Mammals navigating through their environment integrate external sensory cues with self-motion
31 signals such as eye, head and body movements to form an internal estimate of their position in the
32 external world. In the case of vision, extensive studies have investigated the influence of visual cues
33 on neuronal activity classically associated with navigation such as spatial tuning of place and grid
34 cells in the hippocampus and medial entorhinal cortex, respectively [1–5]. However, the impact of
35 navigational signals on visual information processing remains largely unexplored.

36 Due to the development of neuronal recording methods and genetic tools, mice are a powerful
37 animal model to dissect mammalian cortical circuits at the cellular level. Pioneering experiments
38 using the Morris water maze [6,7] have shown that rodents use vision for navigation. While
39 recordings in freely moving rodents have been routinely used for decades for recording hippocampal
40 neurons [5], until recently, most experiments in the visual cortex were performed in head-fixed
41 animals, mainly anesthetized. One reason may be that visual cortical neurons were simply not
42 expected to integrate other stimuli than visual ones and as such, head-fixed settings provided a
43 better control of visual stimulation. The recent development of experimental designs using virtual
44 reality [8,9] and recordings in freely moving animals [*10] have revealed that a significant fraction of
45 neuronal activity in primary sensory areas is modulated by self-motion signals, which could
46 otherwise not be detected in anesthetized animals.

47 In this review, we present recent findings of navigation-related signals in mouse V1, including
48 locomotion, distance travelled, spatial expectations of visual stimuli and head orienting movements.
49 We then review cortical and subcortical areas that have been shown to convey self-motion related
50 inputs to V1 neurons. Recent studies have revealed a key role of somatostatin-positive (SST) subtype
51 of inhibitory neurons in the integration of navigation-related and visual signals in V1 local circuits.
52 We finally discuss potential functional roles of navigation-related signals in V1.

53 **Visual cortex activity is modulated by locomotion, distance travelled and spatial context**

54 Neuronal recordings in head-fixed rodents freely running on a spherical treadmill [11] have revealed
55 that brain-state changes associated with locomotion modulate V1 neuronal activity both in the
56 absence (in darkness) and presence of visual stimuli (Figure 1a, 1b). An increase in running speed
57 correlates with increased pupil dilation and changes in the power spectrum of the local field
58 potential [12,13], as well as an increase in visually-evoked spiking activity of neurons in V1 [9,14–
59 *21] (Figure 1a, 1b) and in higher visual areas [22,23]. In addition, a fraction of V1 neurons was
60 found to be tuned to speed or a weighted sum of speed and visual flow (Figure 1b) [9,15,16].

61 The combination of neuronal recordings in head-fixed rodents with virtual reality is a useful
62 experimental design to test the impact of spatial information on visual responses. A series of
63 experiments have used a visual navigation task in which mice are trained to lick at a given location
64 indicated by a visual cue along a virtual corridor to elicit a reward [**24] (Figure 1c). After learning,
65 the representation of the reward location strongly increased in V1 with a majority of layer 2/3 V1
66 neurons responding at the reward location (Figure 1c). To determine whether this response was
67 dependent on visual cues, the mice were then tested for the same task without visual cues. This was
68 done by removing the reward-associated visual cue and decoupling the visual flow and running
69 speed such that the mice could not use visual information to determine the reward location.
70 Unexpectedly, a subset of layer 2/3 V1 neurons continued to respond to the expected reward

71 location, despite the animal only having self-motion cues. These neurons responded to the distance
72 travelled toward the expected reward, revealing the occurrence of spatial representations in V1 in
73 the absence of visual cues (Figure 1c) [**24]. These results are consistent with a recent study
74 showing that, similarly to hippocampus, activity in primary visual cortex is modulated by the physical
75 distance traveled in a virtual environment [25]. Furthermore, just as hippocampal place cells, V1
76 spatial responses were also found to be modulated by theta oscillations recorded in the
77 hippocampus [25]. V1 neurons may thus combine visual information with movement-related signals,
78 such as the distance travelled, to estimate an animal's allocentric position. Interestingly, when self-
79 motion and visual cues were in conflict, visual information dominated such that V1 activity remained
80 locked to visual cues (Figure 1c) [**24].

81 In addition to modulation by distance travelled, recent studies have also demonstrated
82 neuronal responses to spatial expectation of visual stimuli in layer 2/3 neurons of mouse V1 [*26]
83 (Figure 1d). Mice were repeatedly presented with a sequence of visual landmarks along a virtual
84 track. A subpopulation of V1 neurons showed spatially modulated responses to the same visual
85 stimulus, evoking responses of different magnitude depending on its spatial location along the
86 virtual track [*26,*27]. This spatial modulation could not be explained by other non-visual signals,
87 including running speed, reward, eye movements and pupil dilation [*27]. After repeated experience
88 in the same virtual environment, a fraction of neurons was found to shift the onset of their response
89 to before the appearance of the stimulus that was initially triggering an evoked response [*26].
90 Consistent with responses to spatial expectation of visual stimuli, V1 layer 2/3 neurons were also
91 found to respond to the omission of an expected stimulus in a trained sequence [*26].

92 These findings indicate that responses to visual stimuli are modulated by locomotion and
93 spatial context such that a response to a given visual stimulus in static conditions might be different
94 than a response to the same visual stimulus during navigation. Indeed, it was shown that the same
95 drifting grating elicited different activity depending on whether it was viewed passively by a
96 stationary animal or whether it was coupled to locomotion in a virtual environment [28]. In addition,
97 a fraction of V1 neurons was found to encode mismatches between running speed and visual flow in
98 experiments in which the visual flow was decoupled from the animal's locomotion in a virtual reality
99 environment [16,29–31].

100 Altogether, these results demonstrate that navigation-related signals modulate V1 activity,
101 both in the presence and absence of visual stimuli.

102 **Vestibular and head movement signals in mouse visual cortex**

103 A limitation of the above studies is that they were performed in head-fixed animals such that the
104 impact of 3D head movements and associated vestibular inputs on visual cortex activity could not be
105 assessed. Seminal experiments have revealed head-motion signals in mouse V1, in darkness (Figure
106 1e(i)), both in mice head-fixed on a rotating platform [**32] and in freely moving mice with a
107 miniature head-mounted video camera combined with chronic multi-electrodes [*10]. Whole-cell
108 recordings in head-fixed mice further revealed that membrane potential responses of V1 layer 6
109 neurons encode the direction and angular velocity of passive horizontal rotation, both in darkness
110 and light [**32], (Figure 1e(i)). These responses disappeared after lesions of the semi-circular canals
111 showing their dependence on vestibular organs, consistent with a previous study showing that
112 vestibular nerve stimulation triggers activity in rat V1 neurons [**32–34]. In the presence of visual

113 stimuli, layer 6 neuronal responses were found to summate the vestibular and visual-motion
114 responses [**32].

115 These findings were confirmed and extended by a recent publication showing that head
116 movements modulate V1 activity across all layers, differently in darkness and in ambient light [**35]
117 (Figure 1e(ii)). This series of experiments showed that passive head rotation (head-fixed mice on a
118 rotating platform) in the dark was associated with an overall decrease of activity in V1 layers 2/3 and
119 4, and with an approximately equal distribution between suppression and excitation of activity in
120 deep layers (layer 5 and 6) [**35]. In contrast, head movements in light triggered a net average
121 increase of neuronal activity across all layers. The authors revealed a relationship between the
122 modulation of neuronal activity by light and the response to head movements: larger suppression of
123 activity by light was associated with a higher facilitation of neuronal responses to head movements
124 [**35] (Figure 1e(ii)). This effect was found to be mediated through deep layer somatostatin-positive
125 (SST) cells that inhibit V1 neuronal activity in response to light; head movements in light suppress
126 SST neurons, thus releasing inhibition on pyramidal neurons during head rotation [**35].

127 Similar luminance-dependent modulation of V1 activity by head movements was found in freely
128 moving mice [**35], consistent with previous results in mice [*10,**32] (Figure 1e(iii)). Recordings
129 of layer 2/3 V1 neurons combined with a head-mounted inertial measurement unit in freely moving
130 rats further identified that V1 neurons were tuned for head movement orientation and head
131 direction [**36,37] (Figure 1e(iii), 1f). Allocentric 3D head direction coordinates are represented in
132 V1 layer 2/3 neurons and can be reliably decoded from neuronal activity (Figure 1f) [37]. While head
133 movements during ambient light were associated with enhanced V1 neuronal activity, fast responses
134 to flashed visual stimuli were suppressed during head movements relative to resting condition. This
135 is consistent with a model in which SST neurons are excited by head movement in the dark (before
136 flashing light stimulation) and inhibit pyramidal neurons [**35].

137 When exploring their environment, rodents synchronize head rotations, whisking and cycles of
138 sniffing [38–41]. Orofacial movements were shown to strongly modulate V1 neurons activity
139 [*42,43]. Notably, navigation-related modulation of sensory inputs is not specific to visual cortex
140 since, for example, spatial signals, head movement and direction tuned cells have also been found in
141 primary somatosensory cortex [44,45].

142 **Circuit mechanisms underlying the integration of navigation-related signals in V1**

143 **○ Cortical inputs**

144 Navigation triggers neuronal activity in multiple brain regions, from brainstem to subcortical and
145 cortical areas, including primary sensory and higher order associative areas. Mouse V1 neurons
146 receive inputs from numerous cortical and subcortical brain regions [**30,46]. Some of the top-
147 down cortico-cortical anatomical pathways have been shown to convey navigation-related inputs to
148 V1 neurons (Figure 2a).

149 Higher visual areas are strongly interconnected with V1. Brain state changes associated with
150 locomotion correlate with a strengthening of functional pathways between V1 neurons and higher
151 visual and motor areas, as well as between neurons in RSC and sensory cortices [47]. In addition to
152 the global effect of locomotion and associated brain state changes on neurons in V1 and higher
153 visual areas, spatial modulation of visual responses was also found both in V1 and higher visual areas
154 [48]. Based on the observation that mouse higher visual areas cover different parts of the visual

155 field, it was suggested that landmark related signals may be processed by visual areas with a
156 prominent representation of the central field, while self-motion related signals would be processed
157 by visual areas with a stronger representation of the peripheral visual field [49].

158 Neurons in V1 receive abundant projections from the anterior cingulate cortex (ACC),
159 including the subdivision area A24b, and secondary motor cortical area (M2), that target layers 1,
160 2/3 and 6 pyramidal neurons and PV inhibitory neurons [**30] (Figure 2a). The connections between
161 V1 and ACC are bidirectional as V1 and higher visual areas also send projections to ACC [50–52].
162 Imaging A24b/M2 axons in V1 revealed that locomotion and the resulting visual flow strongly
163 modulated the activity of these axons [**30]. When head-fixed mice, freely running on a spherical
164 treadmill, were trained in a left-right inverted virtual environment, such that the display of the visual
165 flow was inverted relative to the animal’s movements, M2 axonal activity reversed to match visual
166 flow. Optogenetic stimulation of axons from M2 in V1 triggered turning movements of the head-
167 fixed mice on a spherical treadmill, consistent with the activity of these axons during voluntary
168 turning behavior [**30]. Furthermore, it was shown that bilateral lesions of large portions of M2
169 significantly reduced V1 responses to head orienting movements in freely moving rats, with a
170 stronger reduction of responses in darkness than in light [**36].

171 The largest fraction of presynaptic neurons sending axons to V1 from a non-visual cortical
172 area was found in the retrosplenial cortex (RSC) [**30], a multisensory area in which visual,
173 vestibular, and motor-related responses have been recorded [**32,53–56]. These inputs are
174 widespread through V1 cortical layers [**30,**32,57–59]. A subpopulation of RSC neurons was
175 shown to convey vestibular signals for horizontal rotation to layer 6 neurons in V1 [**32] (Figure 2e).
176 Similar to ACC, connections between RSC and V1 are bidirectional and several studies have shown
177 that RSC neurons are critical for visuospatial integration and spatial navigation [56,60–64]. Since RSC
178 neurons receive inputs from the anterior thalamic nuclei [**32,34,58,65], and the hippocampal
179 formation [66], they likely convey not only vestibular information but also integrated spatial
180 navigation-related inputs to V1 neurons. Consistent with this connectivity, a high correlation was
181 found between spatial signals in CA1 and V1 [67,68]. Simultaneous recordings in mouse V1 and CA1
182 showed highly correlated neuronal activity related to the animal’s spatial location, suggesting that
183 similar spatial information is encoded in both regions [*27]. However, recent studies indicate that
184 the integration of landmarks and path integration during navigation differs in V1, RSC and medial
185 entorhinal cortex, with visual landmark cues dominating in V1 and RSC [**24,69] while path
186 integration having more impact on position estimates in medial entorhinal cortex [70–73] than in V1
187 and RSC [69]. Collectively, these results suggest that the information flow between V1 and cortical
188 areas as well as between cortical areas and hippocampal formation is likely to be bidirectional, with
189 multiple loops, raising the question of where these different signals are integrated [74]. Key brain
190 areas for such multimodal integration may be subcortical thalamic nuclei and the superior colliculus.

191 ○ **Subcortical inputs**

192 Thalamic nuclei projecting to V1 were shown to encode movement-related signals, such as
193 locomotor signals in the dorsolateral geniculate nucleus (dLGN) [15] and visuomotor signals in the
194 lateral posterior nucleus (LPN) of the thalamus [*75] (Figure 2a). However, extensive cortico-
195 thalamic feedback from V1 neurons modulates thalamic activity [76], suggesting a complex
196 information flow between these interconnected areas. Locomotion-related signals were also found
197 in the mesencephalic locomotor region and the basal forebrain (BFB) whose cholinergic neurons

198 broadly target subcortical and cortical regions, including V1 [77] (Figure 2a). Calcium imaging of
199 axonal projections in V1 layer 1 from cholinergic (choline acetyltransferase-expressing) neurons in
200 the basal forebrain and from noradrenergic neurons (dopamine beta-hydroxylase-expressing
201 neurons) from the locus coeruleus has shown that activity in both projections increased along with
202 pupil diameter before the onset of walking [78]. After walking onset, noradrenergic-projections
203 activity began to decay whereas cholinergic-projections activity was sustained during locomotion
204 periods [78]. Both cholinergic [18,79] and noradrenergic [18] inputs to V1 have been shown to
205 modulate locomotion-related responses of pyramidal neurons in V1.

206 The superior colliculus is a midbrain structure that was shown to control spatial orienting
207 [80,81]. Bidirectional connections link the superior colliculus to V1 and responses in mouse V1 were
208 shown to be modulated by superior colliculus inputs [82]. Superior colliculus neurons receive inputs
209 from unidirectional projections from the RSC [58,83,84] and as a result could both integrate and
210 convey information from the RSC to V1. Additionally, superior colliculus neurons have strong
211 projections to the LPN (Pulvinar) [85] and a weaker projection to the dLGN [82] that themselves
212 project to V1 and may thus leads to an indirect modulation of V1 activity during navigation.

213 Finally, it was shown that functional interactions between the cerebellum and the
214 hippocampal formation are required for appropriate spatial processing [86,87]. Since cortico-pontine
215 projections have been shown to provide a di-synaptic pathway from visual cortex to the cerebellum
216 [88,89], it is likely that cerebello-cortical loops may also contribute to the integration of visual and
217 navigation signals.

218 ○ **V1 local circuits integrating navigation-related and visual signals**

219 Recent studies have revealed cell-type and layer specific responses of excitatory and inhibitory
220 neurons to navigation-related signals in mouse V1 (Figure 2). Locomotion was shown to modulate
221 the activity of V1 neurons differently in darkness and during visual stimulation, both in layer 2/3
222 pyramidal and SST neurons suggesting a key role of these inhibitory neurons in gating contextual
223 signals [*21,90] (Figure 1a, 2b). Interestingly, luminance changes were shown to modulate V1
224 neuronal responses to other non-visual inputs, such as responses to auditory stimuli [91] and, as
225 described previously, responses to head movements that were dependent on deep layer SST
226 neurons [**35] (Figures 1e, 2d). In layer 2/3, integration of visuomotor mismatch was also found to
227 involve SST neurons [29] (Figure 2c). These results suggest that SST neurons may gate luminance-
228 dependent responses to non-visual signals in V1. Combining experimental results with
229 computational models integrating temporal dynamics and connectivity of excitatory and inhibitory
230 neurons will be critical to assess the impact of sub-types of inhibitory neuron responses onto V1
231 activity patterns [92–94].

232 Layer-specific integration of locomotion and sensory information was found in both mouse
233 visual [15,95] and barrel cortices [96]. Several studies indicate a critical role for layer 6 neurons in
234 context-dependent modulation of V1 activity. Layer 6 receives extensive cortico-cortical and
235 subcortical inputs exerting a gain-modulatory action on V1 activity [97] (Figure 2a), potentially
236 through fast-spiking interneuron mediated translaminar inhibition [98,99]. However, ablation of PV
237 interneurons did not alter the suppression of V1 neuronal activity by head-movements in darkness,
238 indicating that PV neurons are not mediating the modulation of V1 activity by head movements
239 [**35]. Layer 6 neurons were found to receive vestibular signals from a subpopulation of RSC

240 neurons, eliciting responses to head movements [**32] (Figure 2e). Finally, the modulation of V1
241 activity by hippocampal theta oscillations was found to be more prominent in deep layers [25].

242 As described above, most top-down inputs conveying navigation-related signals target
243 superficial layers, where apical dendrites of pyramidal cells are abundant. Several studies
244 demonstrate a key role of top-down inputs to apical tufts dendrites of pyramidal neurons in the
245 integration of non-sensory information in primary sensory areas [13,100]. Dendrite targeting SST
246 neurons may play a key role in gating such information (see Figure 2b-d). Recent studies have shown
247 widespread apical tuft dendritic activity related to locomotion in V1 layer 5 pyramidal neurons
248 [101,102]. Future imaging experiments with voltage-sensitive indicators may reveal the fine-scale
249 temporal dynamics of top-down and bottom up inputs in these neurons.

250 **Functional relevance of navigation-related signals in V1**

251 What is the function of navigational signals in primary visual cortex? One hypothesis is that they
252 contextualize visual stimuli to increase their detection and recognition, for example to discriminate
253 similar stimuli viewed in different locations. It has been suggested that high arousal and locomotion
254 were associated with a more reliable and accurate encoding of visual stimuli [17,90,95]. Consistent
255 with this idea, the performance of decoders used to infer the properties of visual stimuli was higher
256 when using V1 activity during locomotion rather than stationary periods [90,95].

257 Some movement-related signals may also be integrated in V1 to cancel the effects of self-
258 motion. It was suggested that head-orienting movements in rodents may have the same function as
259 saccadic movements in primates; they would suppress activity in visual areas in order to reduce the
260 distortion of the visual scene that is created by fast movements [**36,103]. While saccadic eye
261 movements have been extensively studied in primates [104,105], the function of head and eye
262 movements in rodents remains largely unknown. Dynamic combinations of head and eye
263 movements in freely moving rodents have been described [10,106], some of which are combined to
264 sample their environment [107] and to estimate distances [108]. Consequently, in freely moving
265 conditions, computations of simple features of stationary objects, such as the orientation of a visual
266 stimulus, require the integration of body, head and eye positions. In addition, both visual and self-
267 motion related inputs need to be integrated to provide an accurate estimation of the animal's
268 position in the environment (allocentric representation).

269 A powerful framework for interpreting the function of movement-related top-down signals
270 to V1 is predictive coding [109–111]. In this framework, a prediction of the visual scene is conveyed
271 from the higher cortical areas to V1 neurons, where it is compared to visual information provided by
272 feedforward inputs [110]. This process requires an internal model of the environment from which
273 predictions are computed and updated when feedforward signals do not match the prediction. One
274 proposed implementation of predictive coding suggests that predictive signals from M2 are
275 subtracted from bottom-up visual input in V1, leading to mismatch neuronal responses [29,**30]
276 (Figure 2c). For example, inputs from M2 may convey a prediction of the visual flow's direction
277 generated from motor movements and cancel the impact of such flow on visual information
278 processing in V1. Consistent with a predictive coding framework, V1 activity was found to deviate
279 from baseline almost 1 s (920 ms) before the onset of head movement, suggesting that these
280 responses were triggered by motor planning signals (prediction signals) or a motor efference copy
281 [**36]. Noteworthy, movement-related signals were found in multiple brain regions and represent a

282 large fraction of the brain's activity in many species including worms, flies, and mice [112]. In
283 addition to predictive coding, these widespread signals likely underlie other functions that are not
284 mutually exclusive such as gain control, reafference cancellation, or distributed motor commands
285 [112].

286 **Conclusion**

287 Experiments in awake head-fixed and freely moving animals have revealed multiple non-visual
288 signals in the primary visual cortex, that could not be recorded in anesthetized animals. The
289 discovery of neuronal responses to locomotion, distance travelled and head-orienting movements in
290 V1 raises the questions of the origin of these inputs, the mechanisms underlying the integration of
291 these inputs with visual information, the information that is read-out by downstream targets and
292 ultimately, the behavioral relevance of these integrated neuronal responses. Across species, both
293 navigation and neuronal integration of sensory and navigation-related inputs may be strongly
294 constrained by the ecological environment, species-specific behaviors and brain architecture [112–
295 114, *115]. As such, detailed investigations of natural animal behaviors and natural stimuli
296 [114,*115, 116,117] are necessary to reveal which visual and navigation-related inputs are relevant
297 within an ethological context. Future studies combining behavioural tracking tools [*10,118–120],
298 multi-site recordings and optogenetic tools may reveal the contribution of the multiple cortical and
299 subcortical loops involved in the distributed network underlying the integration of visual and
300 navigation-related information.

301

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307

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588 **Figure legends**

589 **Figure 1. Navigation-related signals in rodent primary visual cortex (V1).** (a) Locomotion increases
590 neuronal gain in V1 neurons, enhancing spiking activity both in darkness and during visual
591 stimulation. Based on [14,*21]. (b) A fraction of V1 neurons is tuned to the mouse's speed both in
592 darkness (Left panel, two examples of speed tuning curves) and during the presentation of visual
593 stimuli in a virtual reality (VR) environment (right panel). Neurons displayed different types of speed
594 tuning, corresponding to a weighted sum of the animal's speed (run speed) and visual flow (virtual
595 speed). Right panel, three examples of neurons whose firing rates are modulated by virtual visual
596 flow speed and run speed. Based on [9]. (c) Layer 2/3 V1 neurons respond to distance travelled but
597 remains locked to visual cues when self-motion and visual landmarks are in conflict. Mice were
598 trained in a virtual environment (VR) to lick at a given location indicated by a visual cue (black walls)
599 to elicit a reward. After learning (Expert trace, green), a subset of V1 neurons responded to the
600 location of the expected reward, even in the absence of visual cue (no cue). Decreasing the gain
601 (0.75) between the virtual visual flow and running speed showed that these neurons responded to
602 the expected reward location based on self-motion information (distance travelled). A visual cue was
603 then added further away from the initial learned location, being visible from the expected reward
604 location based on physical distance traveled. Neurons did not respond anymore to the expected
605 reward location based on the physical distance travelled but instead responded to the visual cue,
606 showing that when it is available, visual information takes over self-motion information and drives
607 V1 neuronal responses. Based on [**24]. (d) V1 neurons' responses to identical visual stimuli (B1,
608 B2) are modulated depending on their spatial location along a virtual track. Based on [*26,*27]. (e)
609 (i) Head movement axes (left panel). Average z-scores of firing rates in mouse V1 during passive
610 head movements (head-fixed on a rotating platform) in darkness (blue) and in light (orange). Based
611 on [**35]. (ii) Schematic scatter plot showing that a larger suppression of V1 neurons activity by light
612 (lower luminance modulation index) is associated with a higher facilitation of neuronal responses by
613 head movements (higher vestibular modulation index shift). Based on [**35]. (iii) Three-dimensional
614 head orienting movements in freely moving rats were found to modulate multi-unit firing rate (z-
615 scored) differentially in light and darkness in an axis- and direction dependent manner. CW –
616 clockwise, CCW – counter-clockwise. Based on [**36]. (f) Schematic plot of true and predicted head
617 direction angles. Head direction was predicted from a linear regression model taking as inputs the
618 multiunit activity firing rates from rat V1 neurons. The model performed well above chance and the
619 results were not significantly different between the light and dark conditions. Based on [37].

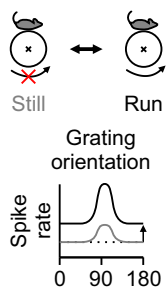
620 **Figure 2. Inputs and local circuits underlying the integration of navigation-related signals in**
621 **primary visual cortex (V1).** (a) Cortical and subcortical inputs conveying navigation-related
622 information to V1. The indicated pathways only include projections which were characterized for
623 conveying navigation- or movement-related information to V1. M2/ACC, secondary motor cortex,
624 anterior cingulate cortex [**30,**36]; RSC, retrosplenial cortex [**32]; HVA, higher visual cortical
625 areas [47]; BFB, basal forebrain [78]; LPN, lateral posterior nucleus [*75]; LC, locus coeruleus [78].
626 (b) Locomotion overall increases the gain of V1 pyramidal cells (PC) activity, and modulates
627 inhibitory neurons' activity differently in darkness and during visual stimulation. Calcium imaging
628 indicates that VIP neuronal activity increases during locomotion in both conditions. Activity of SST
629 neurons was minimally modulated by locomotion in darkness while it was increased by locomotion
630 during visual stimulation. Based on [*21]. (c) Model for visuomotor mismatch computation in V1
631 layer 2/3, established during development through the comparison of visual flow input (dashed blue
632 line) input to SST inhibitory neurons and top-down excitatory motor-related input (dashed green line
633 shows a running period around a mismatch event) to PCs and VIP interneurons. Grey shading
634 represents a mismatch between visual flow and running, during which the visual flow was artificially

635 halted in a virtual reality environment. Dark blue, orange and purple lines show average mismatch
636 responses of PC, SST, and VIP interneurons, respectively. Based on [29]. **(d)** Ambient luminance
637 controls the modulation of V1 activity neurons by head movements through deep-layer SST
638 interneurons: in light, SST interneurons suppress baseline spiking and are inhibited by head
639 movements, thus disinhibiting PCs. In darkness, SST interneurons are excited by head movements,
640 inhibiting PCs. Based on [35]. **(e)** Integration of vestibular and visual-motion signals in V1 layer 6
641 neurons. Postsynaptic responses of layer 6 neurons were found to approximate the arithmetic sum
642 of visual-motion inputs and top-down RSC-derived vestibular inputs during passive head rotation
643 (head-fixed on a rotating platform). Based on [32].

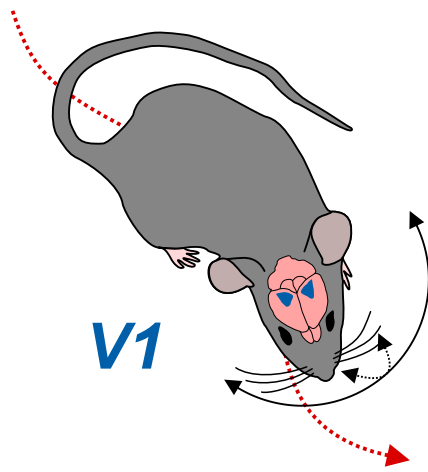
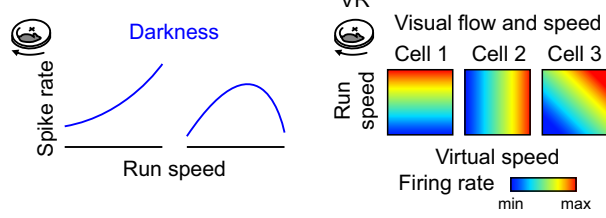
Declarations of interest: none

Figure 1

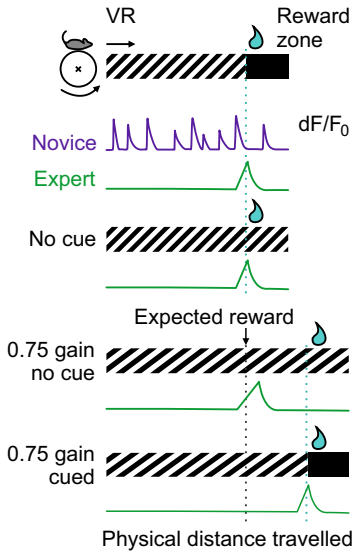
(a) Locomotion



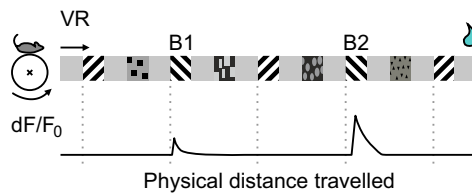
(b) Speed tuning



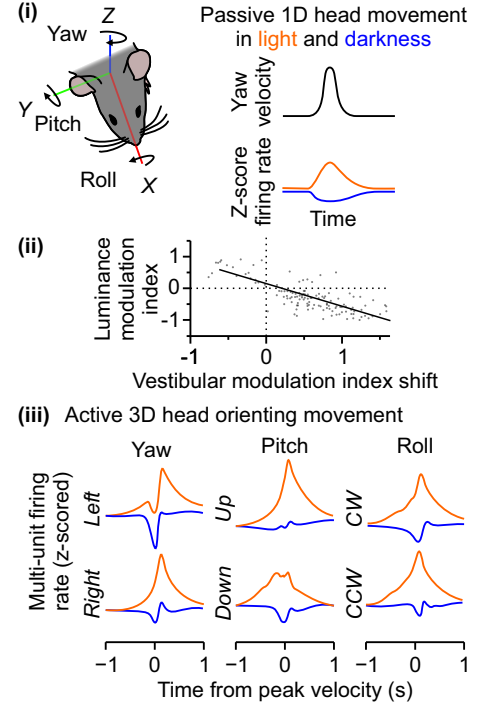
(c) Distance travelled



(d) Spatial location of stimuli



(e) Head movement tuning



(f) Head direction tuning

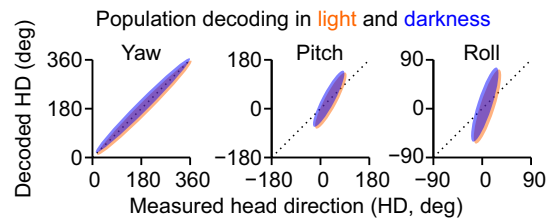
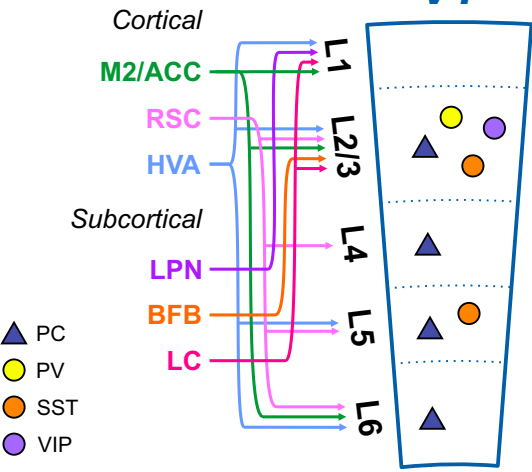
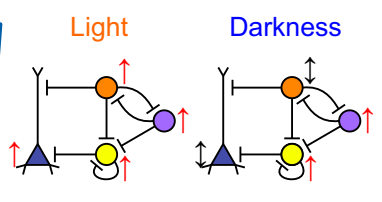


Figure 2

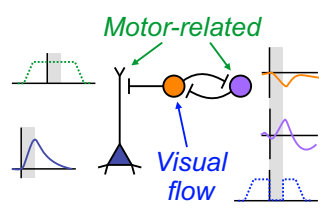
(a) Navigation-related inputs



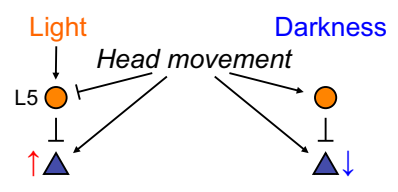
(b) Locomotion



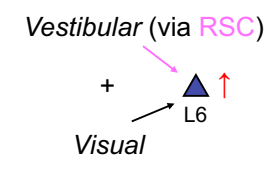
(c) Visuomotor mismatch



(d) Light-dependent response to head movement

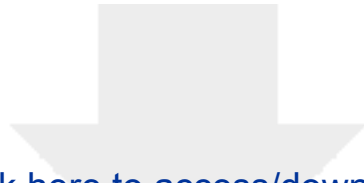


(e) Vestibular and visual motion inputs



Highlights

- V1 activity is modulated by locomotion, distance travelled, spatial context and head-movements
- Top-down cortical and subcortical inputs convey self-motion signals to V1 neurons
- Key role of SST inhibitory neurons in the integration of visual and self-motion signals
- Potential functions of navigation-related signals in V1 include gain control, refference cancellation and predictive coding



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