

processes play a role in the wild, and that the principal research challenge will be to evaluate their relative contributions to these birds' remarkable technologies.

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Superior Colliculus: A Vision for Orienting

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The superior colliculus contains neurons sensitive to motion direction. New research shows that these neurons are anatomically clustered: those representing the region of visual space ‘seen’ by both eyes preferentially respond to nasal motion directions and others to opposite directions.

When we navigate our environment, different parts of our visual field undergo different patterns of luminance and color changes. For example, walking down a corridor, the point farthest away from us moves in an expansive manner on our retinae such that, in the horizontal dimension, we experience motion directed away from our midline, in a so-called ‘temporal’

direction (Figure 1A, left panel, red dashed rectangle). If we were to now turn right, we experience leftward image motion; in our right visual field, such leftward motion is now directed towards our midline rather than opposite it, in a so-called ‘nasal’ direction (Figure 1A, right panel, red dashed rectangle). How different brain circuits process such nasal and

temporal motion signals depends on their functional specializations. A new study by de Malmazet *et al.* [1], reported in this issue of *Current Biology*, has found that direction-selective neurons in the mouse superior colliculus are clustered in a very specific manner: neurons with visual receptive fields representing the binocular zone of the mouse visual field



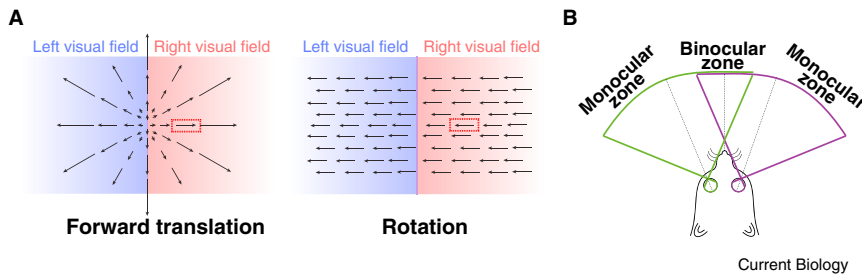


Figure 1. Image motion directions and their relationship to visual field locations.

(A) When translating forward (left panel), image features of objects in our visual field move in an expansive manner as indicated by the black arrows. For a given visual field location (for example in the red dashed rectangle), the motion experienced by the visual system is away from our midline. If we were to turn rightward instead of translating forward (right panel), then the motion that we experience would look different; the same visual field location (for example in the red dashed rectangle) would now exhibit motion towards our midline rather than away from it. de Malmazet *et al.* [1] investigated how superior colliculus neurons process motions like the ones that we might experience when translating or turning in our environment. (B) de Malmazet *et al.* [1] found that, in the mouse superior colliculus, neurons in the binocular zone of the visual field (that is, representing visual field locations projecting light into both eyes simultaneously) preferentially responded to nasal motion directions, whereas neurons in the monocular zone preferentially responded to temporal motion directions.

preferentially signal nasal motion directions; those with visual receptive fields representing the monocularly viewed part of the visual field preferentially signal temporal motion directions. This intriguing observation adds to increasing evidence that, in addition to a spatial representation of visual field locations, the superior colliculus contains multiplexed feature maps that have their own organizational principles.

de Malmazet *et al.* [1] presented visual stimuli to awake mice and simultaneously imaged the activity of individual superior colliculus neurons. They first characterized visual receptive field locations. A visual receptive field is the region in the visual field from which visual signals, like the onset of a light stimulus, elicit neural responses. It has long been known that superior colliculus neurons' visual receptive fields tile locations in the visual field in an orderly manner, something that has been demonstrated in a variety of species [2,3]. The authors then presented moving bars to the mice and investigated how neurons reacted when the bars crossed their receptive fields. A moving bar has both an orientation and a motion direction. In their study, de Malmazet *et al.* [1] moved the bar orthogonal to its orientation: for example, a vertical bar

moved along a horizontal direction, and a horizontal bar moved along a vertical direction, and so on. If a neuron was sensitive to orientation, then it would respond equally well to a bar of its preferred orientation regardless of motion direction, for example to a vertical bar moving either rightward or leftward. On the other hand, if a neuron was direction selective, then it would respond to only one motion direction, for example to a vertical bar or a spot of light moving rightward but not leftward. The authors found that orientation selectivity was independent of direction selectivity, and they confirmed that this independence is not necessarily true in all visual brain areas. For example, in the primary visual cortex, preferred motion direction was orthogonal to preferred orientation.

Most interestingly, direction selectivity was organized highly systematically. Specifically, because mice have two eyes displaced from each other, like us humans, their visual field may be characterized as having two 'zones': in the binocular zone, light from a single visual field location is able to reach both eyes simultaneously; in the monocular zone, only one eye is able to capture light from the environment (Figure 1B). The two zones are useful for a variety of complementary aspects of visually-

guided behavior. For example, the binocular zone can provide the visual system with image disparity information between the two eyes, which is critical for depth perception. On the other hand, the monocular zone can be useful for detecting potential predators in the very far periphery. de Malmazet *et al.* [1] found that superior colliculus neurons representing the binocular zone prefer nasal motion directions, whereas neurons in the monocular zone prefer temporal motion directions. This anatomical clustering of direction sensitivity indicates that a feature map for direction processing is overlaid in the superior colliculus over the existing visual receptive field map of spatial locations. Similar clustering has been observed for orientation selectivity maps in the mouse superior colliculus, again multiplexed with spatial topography [4,5].

The idea that multiple feature dimensions are multiplexed in a single visual brain area is accepted in the case of the cortex. For example, the primary visual cortex multiplexes features like location, orientation, color, spatial frequency, and eye-of-origin in a single brain area (for example [6]). The interesting results from the mouse superior colliculus in the present study [1], as well as in other recent ones [4,5], fit well with this view. Even in primates, in which the historic perspective has been that the superior colliculus is primarily a gaze control structure [7], evidence is emerging that the superior colliculus possesses visual pattern analysis machinery. The primate superior colliculus exhibits tuning for spatial frequency [8–10], orientation [11], and temporal frequency [11]. Moreover, the idea of distinct zones of specialization — like the monocular versus binocular zones mentioned above (Figure 1B) — still holds in primates. For example, representation of the upper visual field is functionally distinct from that of the lower visual field in the macaque superior colliculus [10]. In the future, it should prove highly interesting if feature maps of the primate superior colliculus were explored at the same level of detail as has been done in species such as the mouse [1,4,5,12,13] and zebrafish

[14,15], reviving earlier attempts along these lines [16,17]. This will certainly clarify the utility of having an orienting structure like the superior colliculus possess, simultaneously, its own visual pattern analysis machinery: a ‘vision’ for orienting.

An additional intriguing aspect of the presence of visual feature maps in the superior colliculus relates to the potential role of this structure in computing image salience. The contribution of the superior colliculus to visual attention [18] suggests that it computes the location of salient stimuli, potentially even irrespective of their underlying features [19]. However, feature-specific salience can also be represented. For example, the mouse superior colliculus highlights local motion contrast — motion in one direction flanked by motion in the opposite direction [13] — which can allow objects moving against a background to ‘pop-out’ and be easily detected. It would be interesting to know if there is clustering in this feature-specific salience computation similar to the clustering present in direction selectivity found here by de Malmazet *et al.* [1].

In terms of the functional implications of preferential representation of nasal directions in the binocular zone, de Malmazet *et al.* [1] cited the differences in image flow experienced by animals between translation and rotation (for example, Figure 1A). One wonders if additional interpretations are possible: for example, if the animals were to converge their eyes for whatever reason, a strong, but spurious, image motion signal in the temporal direction would occur in the binocular zone (converging eyes mean diverging image motions on the retinae). It may be exactly such a divergent temporal motion signal that needs to be ignored by the animals. A preference for nasal, not temporal, motion directions in the binocular zone could therefore be a simple way to discount such a spurious signal, in addition to potential other mechanisms that may exist in the superior colliculus (for example [20] for primates). An important future research question would be to fully investigate the functional significance of the clustering in motion direction

preference found by de Malmazet *et al.* [1].

Finally, the study of de Malmazet *et al.* [1], along with others (for example [4,5,12–15]), highlights a truly remarkable aspect of science. Before the rise of the awake monkey as an attractive animal model in systems neuroscience, the ‘optic tectum’ was primarily studied in nonmammalian species such as birds and frogs from the perspective of it being the primary visual structure in these animals’ brains. With the shift to primate studies, an equally-strong shift in view has taken place, resulting in the superior colliculus being viewed as primarily a gaze control structure. This has led to tremendous advances in our understanding of motor control, as well as related cognitive processes like target selection and attention, but it has meant that other aspects of primate superior colliculus functions, like visual pattern analysis, have not been investigated to an equal depth. Inspired by studies like the new one of de Malmazet *et al.* [1], further studies of the primate superior colliculus will surely follow, bringing us full circle across species, sensory modalities, and output behaviors. Research on the superior colliculus is thus nothing but one great example of the undebatable value of using multiple animal models in neuroscience research.

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