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Vision: Magnified Foveal Representation in Monkey Midbrain

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The superior colliculus is canonically viewed as a controller of extra-foveal gaze. This traditional view of superior colliculus function is challenged by the discovery that it has an expanded foveal magnification, comparable to that in primary visual cortex.

Foveal vision is at the heart of human experience. It corresponds to the central 0–2° of gaze: the vision of what we look at, whether it is reading these words or staring into a loved one's eyes. Its namesake, the fovea, constitutes only ~2% of the retina, but its projection into the visual pathway is magnified immensely. For example, roughly 30% of primary visual cortex is devoted to representing information from foveal inputs [1]. This cortical magnification, coupled with the high density of photoreceptors within the fovea, provides for extreme visual acuity, which primates leverage by incessantly moving their eyes to bring salient objects and the fovea into precise alignment. But where and how the foveal representations interact with the oculomotor machinery to generate the eye movements that are necessary for high acuity visual tasks is quite unclear. This is not due to a lack of knowledge about how precise eye movements are generated [2], but rather to a lack of understanding of how oculomotor structures represent foveal stimuli. As they report in this issue of *Current Biology*, Chen *et al.* [3] have now found an enhanced foveal representation in the superior colliculus, a key oculomotor nucleus in the brain, a discovery that challenges traditional views of how the superior colliculus represents, not just foveal, but all visual space.

The superior colliculus occupies a unique niche in the brain. It receives direct projections from the retina [4] and in turn projects through only a few synapses to the muscles that control eye movements. It is an ideal structure for studying sensory-motor transformations and indeed the study of visual-motor representations within the superior colliculus has long been a very active and productive field of research in neuroscience. A coarse motor map was initially found by stimulation of the superior colliculus as long ago as 1872 ([5] but see [6]). Work over the next century

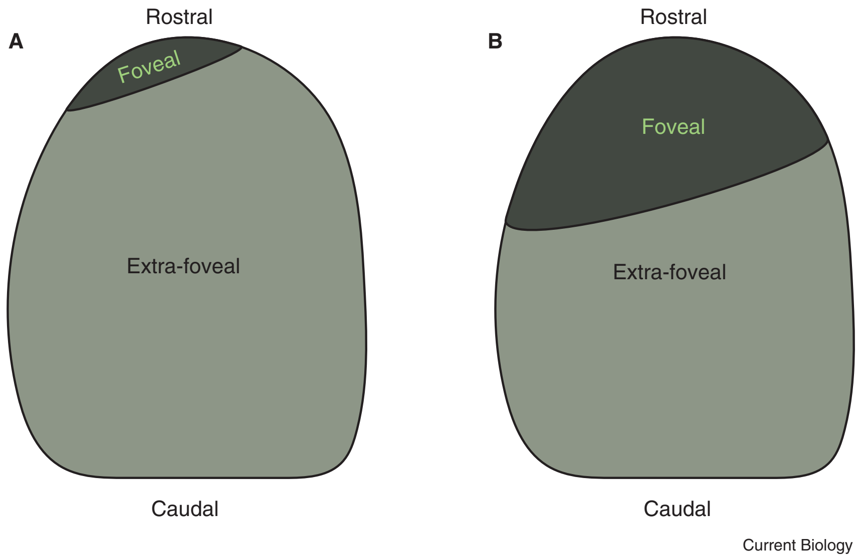

Figure 1. Schematics of the foveal representation within the superior colliculus arising from different datasets.
(A) A top down view of the superior colliculus. The foveal representation is just a sliver of the rostral superior colliculus and likely emerged from the sparse sampling of the rostral superior colliculus in [6], the dataset used to generate the universally accepted map [7]. (B) A schematic of the foveal representation within the superior colliculus based on the new findings of Chen *et al.* [3]: they densely sampled the superior colliculus and revealed a large foveal magnification.

refined the motor map and discovered an overlapping map of visual space; that is, specific positions in the superior colliculus are responsible for both representing visual stimuli within and moving the eyes towards a particular region of visual space. This work culminated in a keystone study [7] that defined the visuomotor topology of the superior colliculus and, since the map's publication in 1986, it has been referenced ubiquitously. This map demarcated only a slight magnification of foveal representation in the rostral superior colliculus (Figure 1A), which led to the interpretation that the superior colliculus is essentially an extra-foveal structure.

Work investigating microsaccades over the past decade, however, started to question the extra-foveal nature of the superior colliculus. Microsaccades are miniscule eye movements that occur even during gaze fixation and the rostral superior colliculus plays a role in their generation [8]. Moreover, microsaccades precisely relocate gaze during high acuity visual tasks [9], which implies sensory inputs drive microsaccades to precisely align objects with the most sensitive parts of the retina. The visual signals driving precise microsaccades could originate within the superior colliculus, but the foveal representation within the superior colliculus is largely unexplored, aside from coarse descriptions from functional imaging studies [10]. It is ironic that microsaccades motivated the study of foveal vision, given they have been notorious for impeding the study of foveal vision: they instigate small displacements of the visual scene which wreak havoc on attempts to record consistent foveal responses.

Chen *et al.* [3] meticulously controlled for small eye movements as they laboriously sampled the response of neurons in the monkey superior colliculus to tiny visual stimuli. Strikingly, they found a substantial population of neurons in the rostral superior colliculus that responded vigorously to foveal stimuli. These neurons had sparse visual fields that tiled foveal space. This population of neurons likely provides the high-fidelity signals necessary to drive precise gaze alignment in high acuity vision. Importantly, these data were used to generate a map of visual space, in a similar fashion to Ottes *et al.* [7], which showed that a quarter to a third of the superior colliculus is dedicated to representing foveal inputs (Figure 1B). This is a much larger fraction than has been assumed since 1986. Indeed, the foveal magnification in the superior colliculus is comparable to that in the primary visual cortex [3], a canonically foveal structure. These results signify a fundamental paradigm shift: the superior colliculus contains a substantial foveal representation and participates in active foveal perception.

In addition to their role in foveal vision, microsaccades have a profound, and perplexing, effect on peripheral vision. Microsaccades modulate responses to visual stimuli in a complex manner that depends on both the timing and direction of the movement [11], and they can even distort the perception of space: the position of a cue is mislocalized if it is preceded by a microsaccade [12]. Chen *et al.* [3] provide a potential mechanism for this distortion, reporting that microsaccades induce a transient but directionally consistent shift in receptive fields. Remarkably, these effects extend to most of the oculomotor range [13]. How do eye movements of just a fraction of a degree alter the response of neurons with receptive fields that span an order of magnitude larger space? These far-reaching effects of microsaccades are particularly difficult to explain with conventional visuomotor topography [7] but there may be clues to an answer in the results of Chen *et al.* [3]. A direct implication of foveal magnification is that peripheral representations are physically closer to foveal representations. So even though peripheral targets are distant in visual space, through magnification they are more proximal to foveal superior colliculus neurons, and this proximity likely facilitates interactions.

Although typically discussed in the domain of vision, the superior colliculus responds quite promiscuously and is instrumental to perceptual and cognitive phenomena across multiple modalities. Chen *et al.* [3] mapped the representation of visual space, but the superior colliculus also contains representations of motor [6,7], auditory [14] and somatosensory [15] space. Future work will need to address the interaction of the visual map with these other representations of space. Do foveal neurons exhibit multi-modal responses, and if so, do they exhibit characteristic multi-sensory integration principles [16]? Moreover, it has become apparent that the superior colliculus is involved in decision making [17] and attentional processing [18]. These studies typically measure cognitive modulation of activity in extra-foveal representations, and it remains to be seen if foveal superior colliculus will exhibit similar cognitive properties. The magnified foveal representation will, at the very least, likely play a substantial role in attention, given recent work showing selective attention within foveal vision [19] and the known interactions between microsaccades and covert selection [11]. Investigating all the implications of such a fundamental shift in the understanding of how the superior colliculus represents visual space will take many years of work.

Moving the eyes to leverage high-acuity foveal vision is inherent to how humans explore and perceive visual environments. Chen *et al.* [3] shift the superior colliculus narrative by showing it is a key player in active foveal perception. Regrettably, over the past few decades few studies have attempted to investigate this fundamental aspect of vision. This is in large part due to the difficulty imposed by fixational eye movements, but another factor has been the shift to model organisms, such as the mouse, that do not possess a fovea. Hopefully, the recent advancement in stimulus presentation [20] and the intriguing results from Chen *et al.* [3] will reinvigorate the field to study a critical part of human experience, foveal vision.

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Conservation: Monitoring Elephant Poaching to Prevent a Population Crash

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African elephants are under threat, especially from poaching for illegal ivory trade. New monitoring data show a dramatic increase in elephant poaching in northern Botswana, where the largest remaining population of African elephants resides.

Many plant and animal species have evolved a dependency on the natural services African elephants provide. As the world's largest land mammal with immense resource needs, elephants maintain habitat diversity and disperse seeds of trees important for carbon capture [1–4]. They also provide considerable economic contributions through ecotourism [5]. Nevertheless, between 1979 and 2015, poaching for ivory reduced Africa's elephant population from an estimated 1.3 million to around 400,000 individuals. One can only imagine how such losses impacted this highly intelligent and socially complex species, let alone their ecological communities. Today, nearly half of