NEURAL ACTIVITY

All eyes on attention

Eye movements are neither necessary nor sufficient to account for the neural effects associated with covert attention.

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You are a football player, running at full speed. The ball is at your feet, your gaze and ‘overt’ attention fixed on it. Suddenly, in the corner of your eye, a player from the opposing team appears. You do not move your eyes away from the ball, but your attention shifts to monitoring your surroundings and ensuring the opponent does not get in your way. This ‘covert’ attention allows the brain to keep track of the player without looking at them (Figure 1A).

According to the premotor theory of attention, when you were covertly monitoring the player, your brain was getting ready for (but not necessarily executing) eye movements towards that spot: this motor preparation would be both necessary and sufficient for attention to shift towards the new spatial location. In other words, spatial attention and motor preparation would share the same neural underpinnings. And indeed, activity in these areas is causally linked with how well individuals perform during attentional tasks (Cavannaugh and Wurtz, 2004).

Still, new evidence has revived the idea that spatial attention may be intrinsically linked to eye movements. Even as you were keeping your gaze on the ball, your eyes were never stationary: they constantly moved due to tiny movements, or microsaccades, which shift the center of the gaze around the fixated location (for a review of this topic, see Rucci and Poletti, 2015).

Most likely, these microsaccades were directed towards the player coming your way – indeed, we tend to perform microsaccades towards covertly attended locations as we fixate on a different object. If these small eye movements are absent or directed away from the location which requires covert attention, neural and behavioral changes associated with attention disappear or decrease (Hafed and Clark, 2002; Lowet et al., 2018).

This poses a serious problem to scientists. If generating microsaccades causes modulation of neuronal activity, the very idea of covert attention – where attention shifts without moving the eyes – may no longer be valid. Put differently, if small eye movements are causally linked to a change in attention, is there still room for the very concept of covert attention in our neuroscience handbooks?

Now, in eLife, Gongchen Yu, Richard Krauzlis and colleagues at the National Eye Institute, Bethesda and the University of Pittsburgh report cleverly designed experiments that help...
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Insight

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Yu et al., 2022

Meyberg et al., 2017

Yu et al., 2022

Meyberg et al., 2017

Poletti et al., 2017

Li et al., 2021

Intoy and Rucci, 2020

Yu et al. then compared how neural activity modulation linked to attention differed when microsaccades were absent, directed towards the cued location, or away from it. Dissecting the relative contributions of microsaccades and spatial attention in this way revealed that neural modulation was present irrespective of microsaccades. In fact, it followed a very similar pattern of activity when microsaccades were absent or directed towards the cue (Figure 1C). Taken together, these findings demonstrate that microsaccades are not necessary for attention-related modulation in the superior colliculus.

The results provided by Yu et al. nicely complement previous behavioral studies which suggest that spatial attention can occur in the absence of microsaccades (Li et al., 2021; Meyberg et al., 2017; Poletti et al., 2017). Yet, outside of the lab, we rarely stare at dots on a screen the way test subjects are asked to do. In fact, in ‘real life’, microsaccades are often leveraged to precisely enhance fine spatial vision, and to explore the rich visual details which form the stimuli we hold at the center of our gaze, such as a fast-moving ball (Intoy and Rucci, 2020). Would the neural modulations associated with microsaccades reported by Yu et al. still occur in these more ecological settings? Only further research will be able to tell. In the meantime, this work makes a case for covert attention to remain in our neuroscience handbooks – for now.
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References
Cavanaugh J, Wurtz RH. 2004. Subcortical modulation of attention counters change blindness. The Journal of Neuroscience 24:11236–11243. DOI: https://doi.org/10.1523/JNEUROSCI.3724-04.2004, PMID: 15601929
Goldberg ME, Wurtz RH. 1972. Activity of superior colliculus in behaving monkey. II. Effect of attention on neuronal responses. Journal of Neurophysiology 35:560–574. DOI: https://doi.org/10.1152/jn.1972.35.4.560, PMID: 4624740
Hafed ZM, Clark JJ. 2002. Microsaccades as an overt measure of covert attention shifts. Vision Research 42:2533–2545. DOI: https://doi.org/10.1016/s0042-6989(02)00263-8, PMID: 12445847
Intoy J, Rucci M. 2020. Finely tuned eye movements enhance visual acuity. Nature Communications 11:795. DOI: https://doi.org/10.1038/s41467-020-14616-2, PMID: 32034165

Juan CH, Shorter-Jacobi SM, Schall JD. 2004. Dissociation of spatial attention and saccade preparation. PNAS 101:15541–15544. DOI: https://doi.org/10.1073/pnas.0403507101, PMID: 15489272
Li HH, Pan J, Carrasco M. 2021. Different computations underlie overt presaccadic and covert spatial attention. Nature Human Behaviour 5:1418–1431. DOI: https://doi.org/10.1038/s41562-021-01099-4, PMID: 33875838
Lowet E, Gomes B, Srinivasan K, Zhou H, Schafer RJ, Desimone R. 2018. Enhanced neural processing by covert attention only during microsaccades directed toward the attended stimulus. Neuron 99:207-214. DOI: https://doi.org/10.1016/j.neuron.2018.05.041, PMID: 29937279
Meyberg S, Sinn P, Engbert R, Sommer W. 2017. Revising the link between microsaccades and the spatial cueing of voluntary attention. Vision Research 133:47–60. DOI: https://doi.org/10.1016/j.visres.2017.01.001, PMID: 28163059
Poletti M, Rucci M, Carrasco M. 2017. Selective attention within the foveola. Nature Neuroscience 20:1413–1417. DOI: https://doi.org/10.1038/nn.4622, PMID: 28805816
Rucci M, Poletti M. 2015. Control and functions of fixational eye movements. Annual Review of Vision Science 1:499–518. DOI: https://doi.org/10.1146/annurev-vision-082114-035742, PMID: 27795997
Smith DT, Schenck T. 2012. The premotor theory of attention: time to move on. Neuropsychologia 50:1104–1114. DOI: https://doi.org/10.1016/j.neuropsychologia.2012.01.025, PMID: 22306518
Yu G, Herman JP, Katz LN, Krauzlis RJ. 2022. Microsaccades as a marker not a cause for attention-related modulation. eLife 11:e74168. DOI: https://doi.org/10.7554/eLife.74168