CellPress
Current Biology
Dispatches

Visual Perception: Attending beyond the Eyes' Reach

Marisa Carrasco* and Nina M. Hanning
Department of Psychology and Center for Neural Science, New York University, New York, NY 10003, USA
*Correspondence: authormarisa.carrasco@nyu.edu
https://doi.org/10.1016/j.cub.2020.08.095

It has been long debated whether visual attention can shift covertly, decoupled from programming eye movements. Now we know that patients with gaze paralysis show conventional benefits of exogenous (involuntary) attention, confirming that covert attention is not driven by oculomotor programming.

You are crossing a busy street. There is no way you can process all the available visual information. You focus your attention straight ahead to navigate among pedestrians. All of a sudden, a car whose driver missed the stop sign appears at the edge of your visual field. Your safety requires perception and immediate action. Fortunately, we are equipped with an attentional orienting system that quickly and automatically prioritizes processing of salient visual events [1], like suddenly approaching cars. According to the *premotor theory of attention* [2], attention shifts are the consequence of motor system activation; i.e., attention is deployed by preparing, but not executing, a corresponding eye movement. Thus, based on this theory, although the car is saliently visible, your attention could not be deployed there because it is so far out in your periphery that it is outside your eyes' reach (Figure 1A). Empirical support for the premotor theory is mixed. Some studies have shown that covert attention can be decoupled from eye movement programming, and that their effects on perception and visual representation differ. A new study by Masson and colleagues [3] reported in a recent issue of *Current Biology* reveals that patients with gaze paralysis, Moebius syndrome, show conventional exogenous (involuntary) attentional shifts notwithstanding the fact that they can neither move their eyes nor plan eye movements in the paralyzed direction. This finding confirms that eye movement planning is not necessary for covert attention deployment, which further challenges the premotor theory of attention.

Covert attention helps us monitor the environment and can inform subsequent eye movements. There are two types of covert attention: endogenous — a voluntary system that corresponds to our ability to willfully monitor information at a given location — and exogenous — a faster and involuntary system that corresponds to an automatic orienting response to a location where salient events are occurring [1]. The original premotor theory postulated that any shift of spatial attention depends on preceding motor activation [2]. Subsequent studies have shown that both neurotypical participants [4] and patients suffering from congenital opthalmoplegia (impaired elasticity of the eye muscles) [5] can deploy covert endogenous attention to locations even beyond their eyes' reach. Based on these findings, a limited version of the premotor theory states that only exogenous attention depends on motor preparation [6].

Masson *et al.* [3] now provide a proof of concept that also covert exogenous attention can be deployed without planning eye movements. Moebius syndrome is a very rare congenital neurological condition (1 in 50,000–100,000 births) characterized by oculomotor disorders, including gaze paralysis. This condition is due to hypoplasia of the lower brainstem, a tiny brain region containing cranial nerves involved in the execution of eye movements [7]. According to the authors [3], patients with this syndrome should not be able to program gaze shifts, as their congenital inability to move the eyes prevents the development of efficient programming of saccades (quick, conjugate movements of both eyes between stable fixations). Support for their premise is provided by findings that children's saccades take longer and are less precise than those of adults, and that efficient saccade programming requires some learning by trials, errors, and adaptation (e.g., [8]). Several authors, including proponents of the premotor theory, assert that peripheral paralysis — a model system for investigating the oculomotor role in covert attention — should prevent exogenous covert shifts of attention (e.g., [4–6,9]).

In the focal study, three patients with congenital horizontal or vertical gaze paralysis performed a detection task (description in Figure 1B). These patients showed conventional benefits indicative of attentional shifts towards the cued location (faster responses for the stimulus at the attended than the unattended location), even for detection stimuli outside their eyes' reach. The two patients with horizontal paralysis showed this benefit in their paralyzed direction with the same temporal profile as neurotypical controls (present at 100 ms, diminished at 300 ms). The timing of this effect is consistent with many studies with neurotypical participants; attention peaks 80–120 ms after cue presentation and is no longer effective shortly thereafter [1]. The patient with vertical paralysis showed a similar, albeit delayed benefit ($\sim$300 ms in the paralyzed direction). This delayed exogenous orienting along the paralyzed axis for patients with vertical gaze paralysis has been interpreted as a close link between covert attention and saccadic programming [9]. Despite this delayed attention shift of the patient with vertical paralysis, taking together the results of the three patients, the focal study challenges the view that the oculomotor system is the driving source of covert attention [2,6].

According to the premotor theory, motor preparation by any effector system can trigger shifts of spatial attention [2]. Given that individuals with oculomotor paralysis typically direct their gaze by executing saccade-like head movements, Masson *et al.* [3] tested a patient with

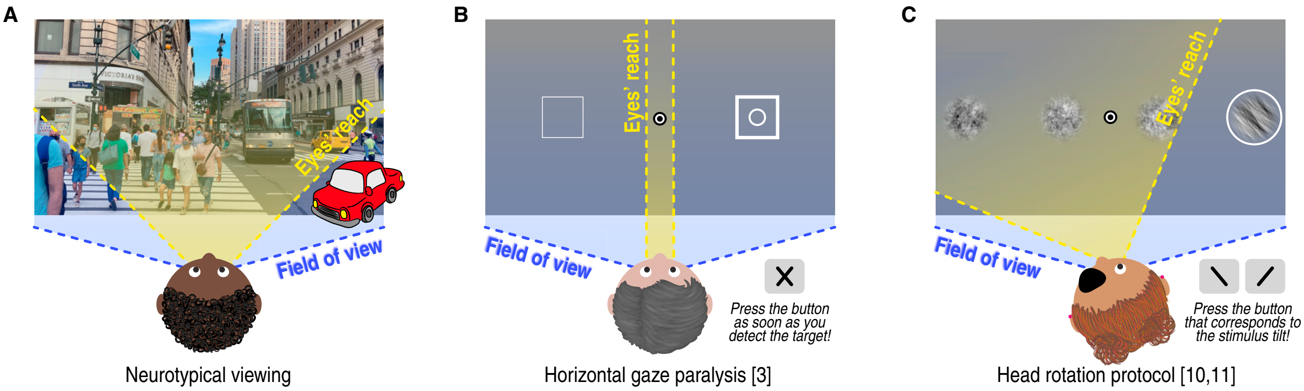

Figure 1. Perception within and beyond the eyes' reach.
(A) Neurotypical viewing (see introductory paragraph). (B) Illustration of a patient in the focal paper. While looking straight ahead, participants were asked to detect a stimulus, which could appear either in the left or right frame. The stimulus was detected faster when preceded by a cue (thickened frame). (C) Illustration of a neurotypical participant in the head rotation protocol. Four noise patches were presented, one containing an orientation signal. The eyes could not reach the outer right patch due to head rotation. The orientation was discriminated better when preceded by a cue (white frame).

horizontal paralysis with a neck abduction protocol (similar to the one used in other studies [4,10,11]; Figure 1C). They found the same attentional effect regardless of whether the stimulus was presented within or beyond the head movement range. Thus, they concluded that covert attention shifts in patients who are incapable of performing eye movements cannot be explained by head movement programming.

Whereas special populations provide us with a natural experiment to test specific hypotheses and to get insights into the underlying mechanisms for perceptual and cognitive mechanisms, the conclusions drawn from them are limited. Most special populations have co-morbidities; for example, patients with Moebius syndrome also suffer facial paralysis [7]. Moreover, given their incapability to perform eye movements, these patients may rely on covert attention more than the neurotypical population. Co-morbidities may also explain the conflicting results between the focal study [3] and earlier studies reporting attentional deficits at locations to which participants could not shift their gaze due to oculomotor pathologies [5,9,12]. For these reasons, it is ideal to have converging evidence from special and neurotypical populations.

Hanning (co-author here) and Deubel recently measured visual sensitivity to investigate the link between eye movement control and exogenous orienting in neurotypical individuals [11]. Visual sensitivity is a more direct and interpretable behavioral correlate of attention (as used in many studies; e.g., [1,10,13–18]) than response times because detection-, decision- and response-dependent processes cannot be disentangled in the latter case. The authors experimentally limited the range of eye movements using a head rotation protocol that prevents performing large saccades against the rotation direction (Figure 1C). Participants were instructed to ignore a salient cue flashed inside or outside the reach of eye movements. The finding that the cue automatically captured attention regardless of its location, as indicated by decreased visual sensitivity at uncued locations, demonstrates that exogenous orienting is not limited to locations the eyes can reach. Crucially, when participants were instructed to perform saccades to the cue [10], which fell significantly short when the cue was out of reach, attention was deployed to the cue instead of the actual saccade landing position. This dissociation demonstrates that attention can shift to locations the eyes cannot reach, and is in line with the observation that the intended saccade target, rather than the actual saccadic landing position, receives the presaccadic attention benefit [14,19] (*presaccadic attention* automatically shifts to the saccade target before eye movement onset). Together with the focal study, these studies provide strong converging evidence that the coupling of exogenous attention and eye movement control is less tight than even the limited premotor theory of attention claims [6].

To further compare and contrast overt and covert attention, recent studies in the Carrasco (co-author here) lab [15–18] have explored how presaccadic attention improves performance [10,13–19] and concurrently modulates the representation of featural information [15–18]. They have found increased selectivity (sharpened orientation tuning [16]) and enhanced spatial resolution (shifting spatial frequency tuning toward higher frequencies [16,17]), which facilitate information processing at the upcoming eye landing location. Crucially, these presaccadic effects are not present with covert attention [15–17]. Moreover, although both covert attention and presaccadic attention increase contrast sensitivity, their behavioral effects and underlying computations differ [18].

To conclude, the focal article examining a special population [3], together with studies investigating neurotypical participants, provides converging evidence that covert attention is possible in the absence of eye movement planning [15–18], and beyond the oculomotor range [10,11]. These studies are in accordance with several models of covert attention that are independent of eye movement planning (e.g., [20]). In short, our attentional orienting system quickly and automatically prioritizes salient visual events — protecting us from suddenly approaching cars — without having to program eye movements.

REFERENCES

1. Carrasco, M. (2011). Visual attention: the past 25 years. Vision Res. *51*, 1484–1525.
2. Rizzolatti, G., Riggio, L., Dascola, I., and Umiltá, C. (1987). Reorienting attention across the horizontal and vertical meridians: evidence in favor of a premotor theory of attention. Neuropsychologia *25*, 31–40.
3. Masson, N., Andres, M., Carneiro Pereira, S., Pesenti, M., and Vannuscorps, G. (2020). Exogenous covert shift of attention without the ability to plan eye movements. Curr. Biol. *30*, R1032–R1033.
4. Smith, D.T., Schenk, T., and Rorden, C. (2012). Saccade preparation is required for exogenous attention but not endogenous attention or IOR. J. Exp. Psychol. Hum. Percept. Perform. *38*, 1438–1447.
5. Smith, D.T., Rorden, C., and Jackson, S.R. (2004). Exogenous orienting of attention depends upon the ability to execute eye movements. Curr. Biol. *14*, 792–795.
6. Casteau, S., and Smith, D.T. (2020). Covert attention beyond the range of eye-movements: evidence for a dissociation between exogenous and endogenous orienting. Cortex *122*, 170–186.
7. Carta, A., Mora, P., Neri, A., Favilla, S., and Sadun, A.A. (2011). Ophthalmologic and systemic features in Möbius syndrome: an Italian case series. Ophthalmology *118*, 1518–1523.
8. Crevecoeur, F., and Kording, K.P. (2017). Saccadic suppression as a perceptual consequence of efficient sensorimotor estimation. eLife *6*, e25073.
9. Rafal, R.D., Posner, M.I., Friedman, J.H., Inhoff, A.W., and Bernstein, E. (1988). Orienting of visual attention in progressive supranuclear palsy. Brain *111*, 267–280.
10. Hanning, N.M., Szinte, M., and Deubel, H. (2019). Visual attention is not limited to the oculomotor range. Proc. Natl. Acad. Sci. USA *116*, 9665–9670.
11. Hanning, N.M., and Deubel, H. (2020). Attention capture outside the oculomotor range. Curr. Biol. *30*, in press.
12. Craighero, L., Carta, A., and Fadiga, L. (2001). Peripheral oculomotor palsy affects orienting of visuospatial attention. NeuroReport *12*, 3283–3286.
13. Hanning, N.M., Deubel, H., and Szinte, M. (2019). Sensitivity measures of visuospatial attention. J. Vis. *19*, 17.
14. Wollenberg, L., Deubel, H., and Szinte, M. (2018). Visual attention is not deployed at the endpoint of averaging saccades. PLoS Biol. *16*, e2006548.
15. Rolfs, M., and Carrasco, M. (2012). Rapid simultaneous enhancement of visual sensitivity and perceived contrast during saccade preparation. J. Neurosci. *32*, 13744–13752a.
16. Li, H.H., Barbot, A., and Carrasco, M. (2016). Saccade preparation reshapes sensory tuning. Curr. Biol. *26*, 1564–1570.
17. Li, H.H., Pan, J., and Carrasco, M. (2019). Presaccadic attention improves or impairs performance by enhancing sensitivity to higher spatial frequencies. Sci. Rep. *9*, 2659.
18. Li, H.H., Pan, J., and Carrasco, M. (2020). Different computations underlie overt and covert spatial attention. bioRxiv, https://doi.org/10.1101/2020.07.22.215905.
19. Deubel, H., and Schneider, W.X. (1996). Saccade target selection and object recognition: evidence for a common attentional mechanism. Vision Res. *36*, 1827–1838.
20. Reynolds, J.H., and Heeger, D.J. (2009). The normalization model of attention. Neuron *61*, 168–185.

Gametogenesis: Germ Cells Aren't Just Along for the Ride

Tara M. Finegan[1] **and Dan T. Bergstralh**[1,2,3,*]
[1]Department of Biology, University of Rochester, Rochester, NY 14627, USA
[2]Department of Physics and Astronomy, University of Rochester, Rochester, NY 14627, USA
[3]Department of Biomedical Genetics at the University of Rochester Medical Center, University of Rochester, Rochester, NY 14627, USA
*Correspondence: dan.bergstralh@rochester.edu
https://doi.org/10.1016/j.cub.2020.08.058

A new study explores the mechanical basis of germline encapsulation in *Drosophila* gametogenesis, reporting that it is not driven solely by somatic tissue, as previously assumed, but instead relies on actomyosin-generated force in the germline cells.

Gametogenesis is the process by which precursor germ cells undergo division, meiosis, and differentiation to form mature haploid gametes. In mammals and insects, female gametes are encapsulated by supporting somatic cells to package the fundamental units of female reproduction. Improper packaging of the germline can cause infertility. In *Drosophila* ovaries, the female gamete and its sister germline cells are encapsulated by a simple epithelial monolayer called the follicular epithelium, resulting in a combined structure called an egg chamber. Encapsulation was assumed to be driven by the active migration and intercalation of the somatic follicle cells. New work from Chanet and Huynh [1], published in this issue of *Current Biology*, now reveals that the encapsulated germ cells are not passive, but play an active mechanical role in egg chamber morphogenesis.

Gametogenesis initiates in many organisms via the formation of groups of interconnected germ cells known as germline cysts (Figure 1A). Since the *Drosophila* ovary is relatively accessible, female gametogenesis has been well documented in this system (reviewed in [2,3]). Briefly, germline stem cells divide asymmetrically to produce a self-renewing daughter cell and a differentiating daughter cell called a cystoblast. This process takes place at

