

## REFERENCES

- O'Farrell, P.H., Stumpff, J., and Su, T.T. (2004). Embryonic cleavage cycles: How is a mouse like a fly? *Curr. Biol.* *14*, R35–R45.
- Foe, V.E., and Alberts, B.M. (1983). Studies of nuclear and cytoplasmic behaviour during the five mitotic cycles that precede gastrulation in *Drosophila* embryogenesis. *J. Cell Sci.* *61*, 31–70.
- Chang, J.B., and Ferrell, J.E. (2013). Mitotic trigger waves and the spatial coordination of the *Xenopus* cell cycle. *Nature* *500*, 603–607.
- Novak, B., and Tyson, J.J. (1993). Numerical analysis of a comprehensive model of M-phase control in *Xenopus* oocyte extracts and intact embryos. *J. Cell Sci.* *106*, 1153.
- Tyson, J.J., and Novak, B. (2015). Bistability, oscillations, and traveling waves in frog egg extracts. *Bull. Math. Biol.* *77*, 796–816.
- Afanzar, O., Buss, G.K., Stearns, T., and Ferrell, J.E., Jr. (2020). The nucleus serves as the pacemaker for the cell cycle. *eLife* *9*, e59989.
- Deneke, V.E., Melbinger, A., Vergassola, M., and Di Talia, S. (2016). Waves of Cdk1 activity in S phase synchronize the cell cycle in *Drosophila* embryos. *Dev. Cell* *38*, 399–412.
- Deneke, V.E., Puliafito, A., Krueger, D., Narla, A.V., De Simone, A., Primo, L., Vergassola, M., De Renzis, S., and Di Talia, S. (2019). Self-organized nuclear positioning synchronizes the cell cycle in *Drosophila* embryos. *Cell* *177*, 925–941.e17.
- Vergassola, M., Deneke, V.E., and Di Talia, S. (2018). Mitotic waves in the early embryogenesis of *Drosophila*: Bistability traded for speed. *Proc. Natl. Acad. Sci. USA* *115*, E2165–E2174.
- Hayden, L., Hur, W., Vergassola, M., and Di Talia, S. (2022). Manipulating the nature of embryonic mitotic waves. *Curr. Biol.* *32*, 4989–4996.
- Edgar, B.A., Sprenger, F., Duronio, R.J., Leopold, P., and O'Farrell, P.H. (1994). Distinct molecular mechanisms regulate cell cycle timing at successive stages of *Drosophila* embryogenesis. *Genes Dev.* *8*, 440–452.
- Su, T.T., Sprenger, F., DiGregorio, P.J., Campbell, S.D., and O'Farrell, P.H. (1998). Exit from mitosis in *Drosophila* syncytial embryos requires proteolysis and cyclin degradation, and is associated with localized dephosphorylation. *Genes Dev.* *12*, 1495–1503.
- Huang, J., and Raff, J.W. (1999). The disappearance of cyclin B at the end of mitosis is regulated spatially in *Drosophila* cells. *EMBO J.* *18*, 2184–2195.
- Raff, J.W., Jeffers, K., and Huang, J.-Y. (2002). The roles of Fzy/Cdc20 and Fzr/Cdh1 in regulating the destruction of cyclin B in space and time. *J. Cell Biol.* *157*, 1139–1149.
- Pines, J., and Hagan, I. (2011). The Renaissance or the cuckoo clock. *Philos. Trans. R. Soc. B Biol. Sci.* *366*, 3625–3634.
- Clute, P., and Pines, J. (1999). Temporal and spatial control of cyclin B1 destruction in metaphase. *Nat. Cell Biol.* *1*, 82–87.
- Murray, A.W., and Kirschner, M.W. (1989). Cyclin synthesis drives the early embryonic cell cycle. *Nature* *339*, 275–280.
- Murray, A.W., Solomon, M.J., and Kirschner, M.W. (1989). The role of cyclin synthesis and degradation in the control of maturation promoting factor activity. *Nature* *339*, 280–286.

## Ensemble perception: Stacking the hay to find the needle

David Whitney<sup>1,\*</sup> and Mauro Manassi<sup>2</sup>

<sup>1</sup>Department of Psychology and Helen Wills Neuroscience Institute and Vision Science Program, University of California at Berkeley, Berkeley, CA 94720, USA

<sup>2</sup>School of Psychology, University of Aberdeen, King's College, Aberdeen, UK

\*Correspondence: [dwhitney@berkeley.edu](mailto:dwhitney@berkeley.edu)

<https://doi.org/10.1016/j.cub.2022.09.042>

The visual clutter we constantly encounter in the world limits object recognition, a phenomenon known as visual crowding. A new study shows that ensemble perception counters this by condensing redundant information into summary statistical representations, which thus releases visual crowding's effect on individual objects.

The visual world is a cluttered place; every visual scene is rife with features and objects of all kinds. The very richness of typical visual scenes is problematic, however, as it is potentially overwhelming for the human visual system. One of the manifestations of the torrent of clutter in the visual field is a perceptual phenomenon known as 'visual crowding'<sup>1–3</sup>. Crowding is a ubiquitous effect in which features and objects appear jumbled together in the presence

of nearby features and objects (Figure 1A). Along with the rampant clutter in the visual world — and its associated crowding effects — the usual existence of multiple similar objects and features means there is generally a great deal of redundancy in natural scenes. For example, consider collections of leaves in a tree, groups of faces in an audience, runners in a marathon, and so on. Fortunately, the visual system is able to harness these redundancies by encoding

the ensemble or summary statistical information that is present in these scenes<sup>4</sup>. Thus, ensemble perception allows us to perceive average features such as color, motion, shape, and facial expressions of crowds (Figure 1B). Ensemble perception is an efficient heuristic to access group-level information at a quick glance, without the need to scrutinize every individual object. A paper in this issue of *Current Biology* by Tiurina *et al.*<sup>5</sup> demonstrates that these



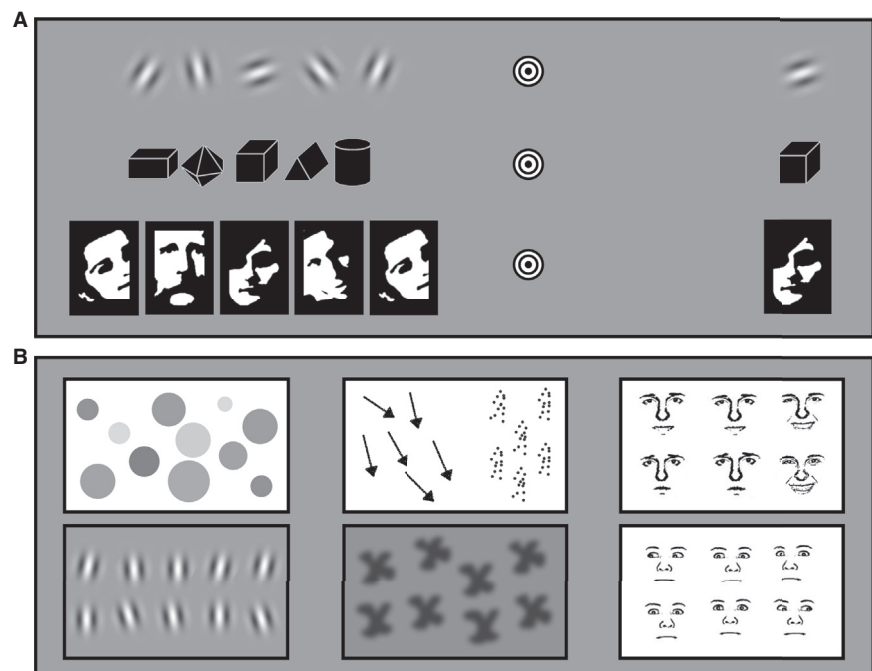
ensemble percepts can gate or modulate how crowding happens (Figure 2).

The results pave the way toward understanding the delicate balancing act the visual system manages between the competing goals of recognizing particular objects in clutter and recognizing the clutter itself.

To demonstrate how ensemble perception modulates crowding, Tiurina *et al.*<sup>5</sup> modified a display from Manassi *et al.*<sup>6</sup> in which a target object was crowded by surrounding flankers (see Figure 2C for example). The clever manipulation was to choreograph the surrounding flankers into an ensemble: when those surrounding flankers were, themselves, seen as part of an ensemble — part of a larger group that is perceived as a single configuration — the flankers were effectively canceled out, and crowding on the single object was released (Figure 2D). In other words, the target was recognizable again, by virtue of the ensemble properties of the visual environment.

Tiurina *et al.*<sup>5</sup> show that ensemble perception can occur when or before crowding happens. Conversely, there is extensive experimental evidence that crowded features and objects can get through the supposed bottleneck of crowding to subsequently determine an ensemble percept<sup>7</sup>. At first glance, this seems like a paradox. On one hand, the ensemble statistics can occur before crowding<sup>5</sup>. On the other hand, ensemble statistics can also include the crowded feature or object that was inaccessible to conscious report<sup>7</sup>. While these may seem like opposing results, in reality they may be complementary findings. To explain, we first need to briefly recall that crowding happens independently for different features and objects<sup>7,8</sup>, that it is modulated by similarity at the feature or object level<sup>7,9,10</sup>, and that it happens at multiple levels of visual processing<sup>2,7</sup>.

In the findings of Tiurina *et al.*<sup>5</sup>, crowding is released when (and only when) there is a clear ensemble statistic in the nearby surrounding objects. The authors suggest that a normalization process<sup>11–13</sup> could happen before or when the crowding is determined. This follows the ensemble coding model proposed by Haberman *et al.*<sup>11</sup>, expanded by Hochstein<sup>12</sup> and Utochkin *et*



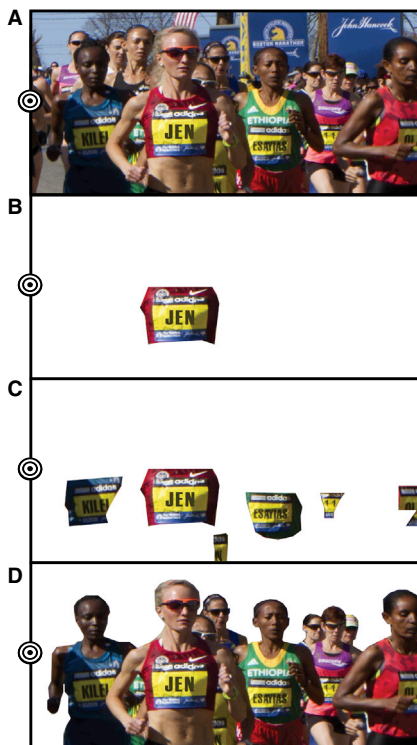
**Figure 1. Two sides of clutter in vision: visual crowding and ensemble perception.**

(A) Visual crowding is the deleterious effect of clutter on object recognition, typically in the peripheral visual field. Fixate the top bullseye and notice that the oriented patches embedded in the clutter on the left are difficult to recognize or identify. The same oriented patch is easy to identify when isolated at an equidistant location (right side of the bullseye). The ‘jumbled’ percept one experiences when objects in the periphery are among clutter is called visual crowding. Crowding occurs for features like orientation (top row) as well as object shape (middle row) and faces (bottom row), among other things. (B) Ensemble perception. Visual clutter in the periphery is often visually similar, and summary statistical information is easily registered in groups of similar things. For example, the average color, orientation, size, motion direction, biological motion, shape, facial expression, and gaze direction are readily recognized in crowds of objects.

*al.*<sup>13</sup>. In the case of similar orientation information in a visual scene (for example, the oriented patches in Figure 1B), a global population response tuning curve is extracted based on a subset (or the whole set) of locally orientation-selective tuning curves. This global population curve represents the average of local tuning curves, and it produces an ensemble percept. Importantly, the resulting global population response then normalizes the local orientation-selective units via feedback or horizontal connections. Any oddball or deviant local tuning curve (for example, an aberrant oriented patch) then pops out, and is uncrowded. Although most models of this sort<sup>11–13</sup> focus on orientation, the same sort of normalization process would happen at every stage where an ensemble representation is formed (for example Chaney *et al.*<sup>14</sup>). Notably, this predicts that summary statistics about any particular feature (such as orientation,

color, or motion) or object (shape, identity, and so on) may release crowding for that particular feature or object — for example, the ensemble biological motion of the crowd in Figure 2 might release crowding of the name on the runner’s bib. Indeed, this is a prediction that could extend the results of Tiurina *et al.*<sup>5</sup>; manipulating summary statistics of other features, objects, or faces could modulate crowding.

Visual crowding is theoretically and practically important for a variety of reasons: it is associated with visual and cognitive impairments<sup>1–3</sup>, it limits human performance in critical everyday tasks like driving<sup>15</sup>, and it sets a fundamental limit on object recognition and conscious vision<sup>2</sup>. Given the many practical and health-relevant consequences of visual crowding, the link between ensemble perception and crowding revealed in the study from Tiurina *et al.*<sup>5</sup> may have significant repercussions. For example,



**Figure 2. Ensemble perception can release crowding.**

(A) Natural scenes are filled with redundant types of information, which are perceived in the form of ensemble statistics (average color, shape, facial expression, and so on). Tiurina *et al.*<sup>5</sup> show that the ensemble statistics in a scene can modulate crowding. (B) When fixating the bullseye, the name on the label is identifiable, and uncrowded. (C) With flanking clutter nearby, the name on the label appears more jumbled and harder to recognize because of crowding. (D) The authors demonstrate that the addition of contextual ensemble statistical information can reduce crowding. In this case, the summary statistical information is the ensemble of runners who share similar shapes and average biological motion.

crowding is impacted in a variety of disorders such as dyslexia<sup>16</sup>, dyscalculia<sup>17</sup>, amblyopia<sup>18</sup> and autism<sup>19</sup>. Thus, these disorders may have consequential changes in ensemble perception as well. Given the release of crowding by summary statistics<sup>5</sup>, manipulating ensemble information might be a way to relieve the debilitating impact of crowding in these groups.

The relationship between ensemble perception and crowding revealed in Tiurina *et al.*<sup>5</sup> may also be relevant for more practical domains. For example, in medical image perception research, finding an abnormal radiograph or a particular tumor might depend on the

nature of the nearby clutter — other images or other tumors or patterns in nearby regions of the visual field. Because what counts as clutter — what crowds — depends on the summary statistics available in the scene<sup>5</sup>, it may be possible to alleviate some of the deleterious effects of crowding in medical image perception by focusing on the available ensemble information, such as the context, rather than focusing solely on the crowded target lesion. It is also worth noting that summary statistics could amplify crowding if the target falls within the summary statistic itself<sup>20</sup>. In any case, it will be important in future work to consider how ensemble information and crowding could interact in practical and clinical settings.

Tiurina *et al.*<sup>5</sup> have uncovered a causal link between two important phenomena of spatial vision: visual crowding and ensemble perception. Their results show how the interplay between perception of local elements (impaired by visual crowding) and the global properties of a scene (summarized into ensemble perception) are intimately tied to each other. On one hand, ensemble perception makes use of crowded objects, thus allowing us to see the hay even when individual straws go unrecognized. At the same time, when the visual scene is processed as an ensemble, cluttered objects can be released from crowding, showing that our visual system is able to stack the hay to find the needle.

#### DECLARATION OF INTERESTS

The authors declare no competing interests.

#### REFERENCES

- Pelli, D.G., and Tillman, K.A. (2008). The uncrowded window of object recognition. *Nat. Neurosci.* *11*, 1129–1135.
- Whitney, D., and Levi, D.M. (2011). Visual crowding: A fundamental limit on conscious perception and object recognition. *Trends Cogn. Sci.* *15*, 160–168.
- Strasburger, H., Rentschler, I., and Jüttner, M. (2011). Peripheral vision and pattern recognition: A review. *J. Vis.* *11*, 13.
- Whitney, D., and Yamanashi Leib, A. (2018). Ensemble perception. *Annu. Rev. Psychol.* *69*, 105–129.
- Tiurina, N.A., Markov, Y.A., Choung, O.-H., Herzog, M.H., and Pascucci, D. (2022). Unlocking crowding by ensemble statistics. *Curr. Biol.* *32*, 4975–4981.

- Manassi, M., Sayim, B., and Herzog, M.H. (2013). When crowding of crowding leads to uncrowding. *J. Vis.* *13*, 10.
- Manassi, M., and Whitney, D. (2018). Multi-level crowding and the paradox of object recognition in clutter. *Curr. Biol.* *28*, R127–R133.
- Greenwood, J.A., and Parsons, M.J. (2020). Dissociable effects of visual crowding on the perception of color and motion. *Proc. Natl. Acad. Sci. USA* *117*, 8196–8202.
- Kooi, F.L., Toet, A., Tripathy, S.P., and Levi, D.M. (1994). The effect of similarity and duration on spatial interaction in peripheral vision. *Spat. Vis.* *8*, 255–280.
- Farzin, F., Rivera, S.M., and Whitney, D. (2009). Holistic crowding of Mooney faces. *J. Vis.* *9*, 18.
- Haberman, J., and Whitney, D. (2012). Ensemble perception: Summarizing the scene and broadening the limits of visual processing. In *From Perception to Consciousness: Searching with Anne Treisman*, J. Wolfe and L. Robertson., eds. (Oxford: Oxford University Press), pp. 339–349.
- Hochstein, S. (2016). The power of populations: How the brain represents features and summary statistics. *J. Vis.* *16*, 1117.
- Utochkin, I.S., Choi, J., and Chong, S.C. (2022). A population response model of ensemble coding. Preprint at bioRxiv, <https://doi.org/10.1101/2022.01.19.476871v1>.
- Chaney, W., Fischer, J., and Whitney, D. (2014). The hierarchical sparse selection model of visual crowding. *Front. Integr. Neurosci.* *8*, 73.
- Xia, Y., Manassi, M., Nakayama, K., Zipser, K., and Whitney, D. (2020). Visual crowding in driving. *J. Vis.* *20*, 1.
- Bertoni, S., Franceschini, S., Ronconi, L., Gori, S., and Facoetti, A. (2019). Is excessive visual crowding causally linked to developmental dyslexia? *Neuropsychologia* *130*, 107–117.
- Castaldi, E., Turi, M., Gassama, S., Piazza, M., and Eger, E. (2020). Excessive visual crowding effects in developmental dyscalculia. *J. Vis.* *20*, 7.
- Bonneh, Y.S., Sagi, D., and Polat, U. (2007). Spatial and temporal crowding in amblyopia. *Vis. Res.* *47*, 1950–1962.
- Kéïta, L., Mottion, L., and Bertone, A. (2010). Far visual acuity is unremarkable in autism: do we need to focus on crowding? *Autism Res.* *3*, 333–341.
- Parkes, L., Lund, J., Angelucci, A., Solomon, J.A., and Morgan, M. (2001). Compulsory averaging of crowded orientation signals in human vision. *Nat. Neurosci.* *4*, 739–744.