- Mower, J.P., Stefanovic, S., Young, G.J., and Palmer, J.D. (2004). Plant genetics: gene transfer from parasitic to host plants. Nature 432, 165–166.
- Davis, C.C., and Wurdack, K.J. (2004). Host-toparasite gene transfer in flowering plants: phylogenetic evidence from Malpighiales. Science 305, 676–678.
- Davis, C.C., Anderson, W.R., and Wurdack, K.J. (2005). Gene transfer from a parasitic flowering plant to a fern. Proc. Biol. Sci. 272, 2237–2242.
- 11. Stegemann, S., and Bock, R. (2009). Exchange of genetic material between cells in plant tissue grafts. Science *324*, 649–651.
- Won, H., and Renner, S.S. (2003). Horizontal gene transfer from flowering plants to *Gnetum*. Proc. Natl. Acad. Sci. USA *100*, 10824–10829.
- Bergthorsson, U., Richardson, A.O., Young, G.J., Goertzen, L.R., and Palmer, J.D. (2004). Massive horizontal transfer of mitochondrial genes from diverse land plant

donors to the basal angiosperm Amborella. Proc. Natl. Acad. Sci. USA 101, 17747-17752.

- Diao, X., Freeling, M., and Lisch, D. (2006). Horizontal transfer of a plant transposon. PLoS Biol. 4, e5.
- Vallenback, P., Jaarola, M., Ghatnekar, L., and Bengtsson, B.O. (2008). Origin and timing of the horizontal transfer of a *PgiC* gene from *Poa* to *Festuca ovina*. Mol. Phylogenet. Evol. 46, 890–896.
- Silva, J.C., and Kidwell, M.G. (2000). Horizontal transfer and selection in the evolution of P elements. Mol. Biol. Evol. 17, 1542–1557.
- Brown, N.J., Newell, C.A., Stanley, S., Chen, J.E., Perrin, A.J., Kajala, K., and Hibberd, J.M. (2011). Independent and parallel recruitment of preexisting mechanisms underlying C₄ photosynthesis. Science 331, 1436–1439.
- Christin, P.-A., Salamin, N., Savolainen, V., Duvall, M.R., and Besnard, G. (2007). C₄ photosynthesis evolved in grasses via parallel

adaptive genetic changes. Curr. Biol. 17, 1241-1247.

- Christin, P.-A., Salamin, N., Muasya, M., Roalson, E.H., Russier, F., and Besnard, G. (2008). Evolutionary switch and genetic convergence on *rbcL* following the evolution of C₄ photosynthesis. Mol. Biol. Evol. 25, 2361–2368.
- Riera-Lizarazu, O., Rines, H.W., and Phillips, R.L. (1996). Cytological and molecular characterization of oat x maize partial hybrids. Theor. Appl. Genet. 93, 123–135.

School of Biological Sciences, Washington State University, Pullman, WA 99164-4236, USA.

E-mail: eric_roalson@wsu.edu

DOI: 10.1016/j.cub.2012.01.043

Visual Perception: Understanding Visual Cues to Depth

A new study shows that, in vision, object blur can be a more accurate depth cue than stereo disparity.

Jenny C.A. Read

Most amateur photographers will have produced snapshots in which the faces of their loved ones are hazy blurs, while the tree behind is in sharp focus. Blur carries information about the object distance, but this information is usually considered to be weak and qualitative, compared to the sharp, quantitative depth provided by stereo disparity [1]. Indeed, stereo vision is often referred to simply as '3D', and forms the basis of the vivid depth in modern 3D TV and cinema. A study reported in this issue of Current Biology by Held, Cooper and Banks [2] provides evidence that these two cues complement each other - and that blur can sometimes be the more accurate guide to depth.

The simplest possible imaging system, a pinhole camera, samples light rays passing through a single point. In such a system, position in the image indicates the direction from which each light ray came, but there is no unambiguous information about the distance of the object which emitted that light. Nevertheless, even in such a simple system, depth can be deduced from cues such as shading, texture gradients, and perspective. Over the centuries, artists have learnt how to mimic these so as to produce the illusion of depth on the flat surface of a painting. However, these cues

require assumptions about the world, and when these are violated, the results can be misleading (Figure 1).

Distance can, however, be solved for directly if one is able to compare two different light-rays emanating from the same point. This requires sampling the optic array at multiple locations: not one pinhole camera, but several (Figure 2). Our visual systems do this in several ways. For example, we may move our heads so as to sample the optic array at different locations over time. This motion parallax is exploited by birds when they bob their heads back and forth. Second, our two eyes sample the optic array simultaneously at two different locations about 6 cm apart, enabling us to extract the disparity between an object's image-position in the two eyes. Third, our pupils are not pinholes but have



Figure 1. Giant Boy: Ames Room at the Edinburgh World of Illusions.

The room is trapezoidal; the woman is much further from the viewer than the child, and so subtends a similar angle on the retina even though she is much taller. Our brains interpret the perspective information on the false assumption that the room is rectangular. The child therefore appears enormous. Photo by Erika Fanselow.

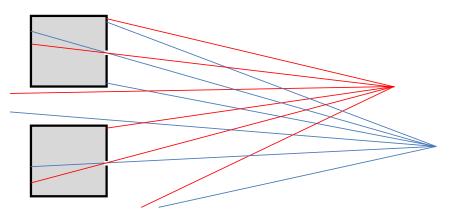


Figure 2. Depth from triangulation.

The optic array at a point consists of all the light rays crossing that point, in all directions. Some example light rays are shown emanating from two point objects, one red and one blue. Two pinhole cameras sample the optic arrays at two different points in space. The locations of the objects can be deduced from where the matching rays in the two pinholes intersect.

a minimum diameter of about 2 mm, so sample a finite range of optic arrays. This requires our lens to accommodate in order to focus light correctly on our retina. Objects out of the focal plane appear blurred (Figure 3). The amount of blur is also a cue to depth.

Although a blurred photo seems verv different from a 3D TV, there are many similarities between disparity and defocus. Both are depth cues which are available from purely retinal information (although they may need extraretinal information, such as eye position or pupil diameter, to be interpreted fully). They are both based on the geometry of light rays, and are thus independent of assumptions about scene statistics (although such assumptions may be necessary in order to pair up left and right image features in order to extract disparities in the first place). Both cues are available instantaneously, in a single binocular image, unlike motion parallax, where information arrives over time. Indeed, defocus can be thought of as reflecting the disparity between optic arrays sampled at either side of the pupil ([3,4]; Figure 1 of [2]). The equations describing them are identical up to sign, with fixation distance mapping to focal distance and interocular separation to pupil diameter.

There are, however, important differences between the two systems. First, disparity triangulates from a wider baseline. Second, whether an object is in front of or behind fixation can be deduced from which eye receives which image. In blur, both images fall in the same eye, so sign information is lost. Third, pupil diameter fluctuates with light level, while interocular separation is constant, complicating the extraction of metric distance (although not relative depth). Perhaps for these reasons, previous studies have concluded that disparity is a much stronger depth cue than blur [1,5,6].

These studies had two limitations. First, they simulated defocus by presenting blurred images at the focal distance. Diffraction, aberrations and chromatic aberration mean that the image of an object at the wrong focal distance is not simply a low-pass filtered version of the focused image. Humans are sensitive to higher-order aberrations, and can use them to discriminate the sign of depth in briefly-presented stimuli [7]. This leaves open the possibility that true optical blur may be a stronger cue than this simulated defocus. Second, they tended to study stimuli near to the fixation/focal plane. Our visual systems only encode disparities up to a degree or so on either side of fixation. It has therefore been suggested that blur may become a more powerful depth cue for objects further from fixation/focus [6]. While plausible, this suggestion has apparently never been tested empirically.

Both issues are addressed in the new study by Held *et al.* [2], who used a novel 'volumetric' display to present images at physically different distances, so blur is introduced by each observer's own optics. In this experiment, the subjects were given eye drops, spectacle lenses and contact lenses which ensured their eyes had a constant pupil diameter and were permanently focused on the fixation point. Subjects were then shown a brief glimpse of two patterned surfaces, both further away than fixation, and asked which appeared furthest. Angular size, brightness and so on were kept constant. Distances were simulated either by binocular disparity alone (with the images presented at the same physical distance, so blur was uninformative). or by blur alone (with the images viewed monocularly, so disparity was unavailable), or by both consistently.

When both stimuli were close to fixation, distance thresholds based on disparity alone were an order of magnitude smaller than those based on blur alone. This confirms that near to fixation/focus, blur is indeed a less reliable cue than disparity, even when higher-order aberrations are available. But in line with previous literature, the distance thresholds obtained with disparity increased steeply as the surfaces being compared moved away from the fixation plane. In contrast, the blur-based thresholds staved roughly constant in centimetres. With fixation at 27.5 cm, once the closer surface was at 30 cm, distance judgments based on defocus were more accurate than those based on disparity. When both cues were informative, thresholds followed the best cue.

This confirms that, indeed, disparity and blur complement each other, with disparity operating near fixation and



Figure 3. Depth from blur.

The camera was focused on the right-hand ladybird; the ladybird on the left is blurred due to defocus, and the grass behind is more blurred still. The shallow depth of field helps to convey the small scale of the scene. Photo by Victoria Clare. Dispatch R165

blur over larger depth intervals. It is important to understand that this complementarity does not arise from the physics, but from the physiology. As Held et al. [2] explain, disparity requires many neurons to encode precisely. Blur is much cheaper to encode, because it does not require custom-built detectors comparing the two eyes, but can use the spatial filters already required for monocular vision [8]. It appears the brain has therefore opted for 'gold standard' depth only near the current point of interest, making do with 'cheap and cheerful' elsewhere.

As Held et al. [2] recognise, their paper addresses only the space in front of and behind fixation; it remains to confirm that blur also improves depth judgements to left and right, or above and below, fixation. Our ability to, say, duck overhanging branches while keeping our eyes on the path ahead suggests that we successfully sense object distances even in our visual periphery, and it would be surprising if blur did not contribute to this too.

The importance of blur has implications for the growing industry of stereoscopic 3D. Held et al. [2] rightly point out that 3D content needs to respect the geometrical relation between blur and disparity. For example, if a shallow depth of field is used to blur large disparities which otherwise might cause double vision, it is important to ensure that the depth of field is correct for the simulated scene [9]; otherwise, objects may appear miniaturised (compare Figure 3). However, it is not clear how successfully defocus can be simulated in a 3D display, given that viewers in non-laboratory situations are free to look around the scene and alter their accommodation. As blur fails to respond correctly to changes in accommodation, objects may be perceived as having strangely fuzzy edges, rather than sharp edges which are out of focus. It remains to be seen whether skilful use of blur in these displays can make large disparities less disturbing and heighten the sensation of depth.

References

- Mather, G., and Smith, D.R. (2002). Blur discrimination and its relation to blur-mediated depth perception. Perception 31, 1211–1219.
- Held, R.T., Cooper, E.A., and Banks, M.S. (2012). Blur and disparity are complementary cues to depth. Curr. Biol. 22, 426–431.
- Schechner, Y.Y., and Kiryati, N. (2000). Depth from defocus vs. stereo: How different really are they? Int. J. Comput. Vision 39, 141–162.
- Adelson, E.H., and Wang, J.Y.A. (1992). Single lens stereo with a plenoptic camera. IEEE T. Pattern Anal. 14, 99–106.
- 5. Mather, G. (1997). The use of image blur as a depth cue. Perception 26, 1147–1158.
- Mather, G., and Smith, D.R. (2000). Depth cue integration: stereopsis and image blur. Vision Res. 40, 3501–3506.
- Wilson, B.J., Decker, K.E., and Roorda, A. (2002). Monochromatic aberrations provide an odd-error cue to focus direction. J. Opt. Soc. Am. A 19, 833–839.
- Burge, J., and Geisler, W.S. (2011). Optimal defocus estimation in individual natural images. Proc. Natl. Acad. Sci. USA 108, 16849–16854.
- Watt, S.J., Akeley, K., Ernst, M.O., and Banks, M.S. (2005). Focus cues affect perceived depth. J. Vis. 5, 834–862.

Institute of Neuroscience, Newcastle University, Henry Wellcome Building, Framlington Place, Newcastle upon Tyne, NE2 4HH, UK. E-mail: j.c.a.read@ncl.ac.uk

DOI: 10.1016/j.cub.2012.01.048

Evolution: Return of the Ant Supersoldiers

An ancient developmental potential to form 'supersoldiers' facilitates the recurrent evolution of this subcaste in various species of *Pheidole* ants.

Benjamin Prud'homme and Nicolas Gompel

Colonies of social insects (ants, bees, wasps and termites) are typically divided into various groups - the castes and subcastes, each with a distinctive morphology and devoted to particular tasks: the queen is the only reproductive female and specializes in producing eggs, while workers forage for food or nurse the queen's progeny, and soldiers protect the nest from attacks. The evolution of complex caste systems and the division of labour are thought to have contributed to the evolutionary success of social insects. However, the developmental mechanisms underlying the origin and evolution of the different castes are poorly understood. Studying the repeated evolution of the supersoldier subcaste in the ant genus Pheidole, a team lead by Ehab Abouheif recently reported in *Science* [1] that the developmental potential to form this subcaste, although dormant in most species, was present in the common ancestor of all *Pheidole* species. This, therefore, facilitated the recurrent evolution of this subcaste in multiple species.

Pheidole species typically comprise two castes, the minor workers and the soldiers [2]. The soldiers have distinctively enlarged heads, which earned *Pheidole* ants their nickname of 'big headed' ants. In a few *Pheidole* species, size variation among soldiers led taxonomists to further divide this caste into two subcastes: simple soldiers and supersoldiers, a bigger version of the former (Figure 1) [3]. In *Pheidole obtusospinosa*, the major function of the supersoldiers is to protect the nest from army ant raids by blocking its entrance with their big heads [4]. Supersoldiers are known in only eight *Pheidole* species that are scattered throughout the family tree [5], a phylogenetic pattern that, at a glance, would suggest independent evolution of the supersoldier subcaste in distinct *Pheidole* species.

To tackle the question of how the supersoldiers evolved, Rajakumar et al. [1] first tried to understand how this subcaste develops. Caste assignment is determined during larval development and is largely controlled by environmental cues such as food: different inputs at particular switch points translate into different levels of juvenile hormone, which in turn modulates developmental trajectories and sets the caste fate of each larva [6]. A first juvenile hormone-mediated switch singles out the future queen from the workers. A second developmental switch, controlled by nutrition, separates minor workers from soldiers that produce more juvenile hormone and therefore grow bigger. But how are supersoldiers specified developmentally?

Rajakumar et al. [1] noticed that in two species forming a supersoldier