

15. Biernaskie, J.M. (2011). Evidence for competition and cooperation among climbing plants. *Proc. R. Soc. B* 278, 1989–1996.
16. Falik, O., Mordoch, Y., Quansah, L., Fait, A., and Novoplansky, A. (2011). Rumor has it...: relay communication of stress cues in plants. *PLoS One* 6, e23625.
17. Trewavas, A. (2014). *Plant Behaviour and Intelligence* (Oxford: Oxford University Press).
18. Novoplansky, A. (1996). Developmental responses of individual *Onobrychis* plants to spatial heterogeneity. *Vegetatio* 127, 31–39.
19. Shemesh, H., Arbiv, A., Gersani, M., Ovadia, O., and Novoplansky, A. (2010). The effects of nutrient dynamics on root patch choice. *PLoS One* 5, e10824.
20. Karban, R. (2015). *Plant Sensing and Communication* (Chicago: University of Chicago Press).

Visual Space: Adaptation to Texture Density Reduces Perceived Object Size

Frederick A.A. Kingdom

McGill Vision Research, Department of Ophthalmology, Montreal General Hospital, 1650 Cedar Ave., Rm. L11.112, Montreal, PQ, H3G 1A4, Canada

Correspondence: fred.kingdom@mcgill.ca
<http://dx.doi.org/10.1016/j.cub.2016.05.068>

A recent study shows that visual adaptation to dense textures, while causing an increase in the perceived sparseness of a subsequently viewed less-dense texture, paradoxically reduces the perceived size of an object, revealing a dissociation between the internal spatial representations of textures and objects.

How do we perceive the spatial relationships of objects in the visual world? One popular tool used by vision scientists to explore this question is adaptation. The distortions experienced in the appearance of objects following adaptation reveal fundamental truths about the mechanics of vision. Two of the best known examples of adaptation-induced distortions are the ‘motion aftereffect’ [1], in which prolonged viewing of a moving object causes a subsequently viewed stationary object to appear to move in the opposite direction, and the tilt aftereffect [2], in which prolonged viewing of a tilted line causes a subsequently viewed vertical line to appear to be tilted in the opposite direction. Because such aftereffects are generally repulsive (the motion-aftereffect is in the opposite direction to the adaptor motion; the tilt aftereffect the opposite orientation to the adaptor orientation), it is widely believed that they result from inhibitory interactions among cortical neurons that are sensitive to the visual dimension in question.

An important visuo-spatial dimension is texture density. Although texture density is tricky to define for smoothly-varying

visual textures, it is relatively straightforward for the mosaics of discreet black and white dots illustrated in Figure 1. For these textures, density is the number of elements per unit visual area — the textures in the figure are said to possess densities of this or that number of dots per square degree of visual angle. As with other visual dimensions, texture density is adaptable: prolonged viewing of a dense texture causes a less dense texture to appear even less dense, or, put another way, more sparse [3–5]. This suggests that there are specialized neurons in the brain for encoding texture density.

So far so good: texture density behaves in a similar manner to other adaptable visual dimensions. A recent study by Hisakata *et al.* [6], however, has revealed a paradoxical effect of texture density adaptation: when the test pattern is a single pair of dots, rather than causing an increase in the perceived dot separation as one might expect, it causes a decrease. Figure 1 illustrates the experimental protocol. Moreover, Hisakata *et al.* [6] show that the ‘shrinking’ effect with dot-pairs extends to geometric forms such as a circle. This is a surprising finding that raises new

questions not only about texture density adaptation, but generally about how spatial relationships are encoded in vision.

Adaptor Density versus Dot-pair Separation

Why do dot-pairs and circles appear to shrink after observers adapt to a texture of dots? For the dot-pair case the first thing to consider are the particular adaptor densities and dot-pair separations in the experiments. Previous studies have hinted that adaptation to texture density only ever causes subsequently viewed textures to appear less dense, implying that the aftereffect is ‘uni-directional’ [7]. The published record on this issue, however, is equivocal, so it is possible that the density aftereffect is in fact ‘bi-directional’, that is, adaptation not only causes less dense textures to appear even less dense but also causes more dense textures to appear even more dense. If the texture density aftereffect were indeed bi-directional, and if the average between-dot separation in the adaptor textures used by Hisakata *et al.* [6] was greater than that of the test dot-pair, then one would expect the test

dot-pair to shrink. Hisaka *et al.* [6], however, used a range of adaptor densities, most of which comprised dots whose separations were on average *less* than that of the test dot-pair, and these would be expected to cause perceptual expansion not shrinkage. Yet shrinkage was observed for all adaptor densities.

Size Adaptation?

Another possible cause is size adaptation. Visual adaptation to a large object causes a subsequently viewed smaller object to appear smaller than otherwise [8]. The adapting textures in Hisaka *et al.*'s study were contained in a window that was larger than the test dot-pair, so if the visual system treated the adapting texture as a large object, the shrinkage in the test dot-pair would be expected. Among other experiments to control for the texture-as-object explanation, Hisakata *et al.* showed that a black frame the size of the texture window presented to both adaptor sides of the adapting field (see Figure 1) failed to eliminate the shrinkage. This suggests that size adaptation is an unlikely cause. Other experiments conducted by Hisakata *et al.* [6] appear to rule out the related candidate of spatial-frequency adaptation, in which the relevant dimension is the frequency with which the luminances of the adaptor dots vary across space.

Depth Adaptation?

Two other possibilities not considered by Hisakata *et al.* are worth mentioning. One is depth adaptation. As an object recedes from view the visual angle it subtends diminishes. Even though Hisaka *et al.*'s [6] dense adaptors were displayed on the plane of the display monitor, it is possible they were perceived as relatively distant textured surfaces, because of the closeness of the dots in the retinal image. Depth is an adaptable feature [9], with adaptation to a far object causing closer objects to be perceived closer than otherwise. Thus, adaptation to the 'depth' of the dense texture might result in the test dot-pair being perceived as closer than otherwise. Our built-in size constancy mechanism, which takes into account both retinal image size

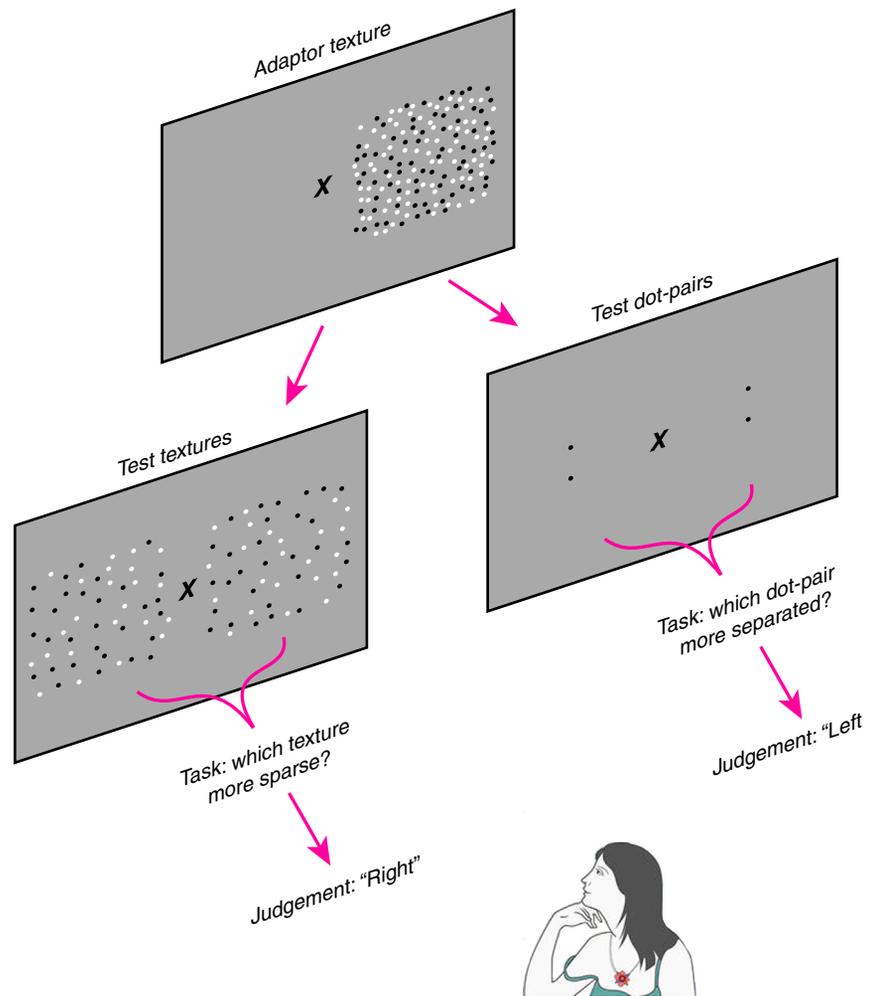


Figure 1. Schematic of two of the experiments conducted by Hisakata *et al.* [6].

In each experiment the observer was required to compare stimuli presented either side of fixation following adaptation to a dense texture on just one side of fixation. The observer's task was to indicate: Left, which stimulus appeared more sparse; Right, which dot-pair appeared more separated. The judgement shows the observer's choice when the stimuli on either side of fixation were physically the same.

and viewing distance when computing the size of an object, would then compute a smaller dot separation than otherwise.

Notwithstanding the obvious rejoinder to this explanation that the requisite depth relations are not readily observed in the stimuli, the explanation would predict that the perceptual shrinkage should systematically increase with adaptor density. Hisakata *et al.* [6], however, found a more-or-less constant effect of adaptor density on perceived dot separation. The depth explanation also cannot explain the contrary result with the

test textures, where the adaptors caused an increase, not decrease, in sparseness.

Dense Textures Expand Visual Space?

Another possibility is that dense textures alter the visual system's internal metric of space, an internal metric that is adaptable. Some years ago Craven & Watt [10] showed that the perceived separation between two parallel lines increases when the space between them is interspersed with other parallel lines. Thus, filling a region with dots might cause a perceptual expansion of the

Current Biology

region. Because of the repulsive nature of spatial adaptation, adaptation to such an expanded region could produce a perceptual shrinkage of a subsequently viewed object. However, as with the depth adaptation explanation above, this cannot explain the opposite direction of effects for the test textures and test objects.

Separate Mechanisms for Coding Density and Object Size

How do Hisaka *et al.* [6] explain their shrinkage results? They opine that perceived distance is computed by summing neural signals that each express a unit of length along the path from one point to another in the image. Adaptation to a dense texture might reduce the perceptual length associated with the length of the unit, akin to the way that contrast adaptation reduces the apparent contrast of subsequently viewed stimuli [11].

Whatever the cause of the shrinkage, it is the fact that it goes in the opposite direction to the texture density aftereffect that is the intriguing and challenging part of Hisakata *et al.*'s [6] study. A possible clue to the resolution of this paradox lies in existing models of texture density coding [12–15]. These models all assume that there is an initial stage in which the markings on a textured surface are 'picked up' by arrays of neurons, such as simple cells in the visual cortex, that are sensitive to the markings' positions, sizes and orientations. Although the details of the models vary as to what comes next, all share the idea that subsequent neural processes convert those responses via a cascade of filtering operations into an explicit representation of density (or relative density). During this process, information about the positions of individual texture markings is lost. In other words the resulting density signal is agnostic to the local position information that gives rise to it. If this view of density coding is correct, something altogether different must be going on when the visual system estimates the separation between parts of an object, as the paradox revealed by Hisaka *et al.* implies.

Although we do not yet have a definitive explanation for the object shrinkage from texture density

adaptation demonstrated by Hisakata *et al.* [6], their study will doubtless set in motion a new line of inquiry into the encoding of spatial relationships in human vision.

REFERENCES

1. Mather, G., Verstratten, F., and Anstis, S. (1998). *The Motion Aftereffect: A Modern Perspective* (London, England: MIT Press, Cambridge Massachusetts).
2. Gibson, J.J. (1937). Adaptation, after-effect, and contrast in the perception of tilted lines. II. Simultaneous contrast and the areal restriction of the after-effect. *J. Exp. Psychol.* **20**, 553–569.
3. Durgin, F.H. (1995). Texture density adaptation and the perceived numerosity and distribution of texture. *J. Exp. Psychol. Hum. Percept. Perform.* **21**, 149–169.
4. Durgin, F.H., and Proffitt, D.R. (1996). Visual learning in the perception of texture: simple and contingent aftereffects of texture density. *Spat. Vis.* **9**, 423–474.
5. Durgin, F.H. (2008). Texture density adaptation and visual number revisited. *Curr. Biol.* **18**, R855–R856.
6. Hisakata, R., Nishida, S., and Johnston, A. (2016). An adaptable metric shapes perceptual space. *Curr. Biol.* **26**, 1911–1915.
7. Durgin, F.H., and Huk, A.C. (1997). Texture density aftereffects in the perception of artificial and natural textures. *Vis. Res.* **37**, 3273–3282.
8. Blakemore, C., and Sutton, P. (1969). Size adaptation: a new aftereffect. *Science* **166**, 245–247.
9. Blakemore, C.B., and Julesz, B. (1971). Stereoscopic depth aftereffect produced without monocular cues. *Science* **171**, 286–288.
10. Craven, B.J., and Watt, R.J. (1989). The use of fractal image statistics in the estimation of lateral spatial extent. *Spat. Vis.* **4**, 223–239.
11. Georgeson, M.A. (1985). The effect of spatial adaptation on perceived contrast. *Spat. Vis.* **1**, 103–112.
12. Durgin, F.H. (1999). A model of texture density encoding. *Invest. Ophthalmol. Vis. Sci.* **400**, S200.
13. Kingdom, F.A.A., Hayes, A., and Field, D.J. (2001). Sensitivity to contrast histogram differences in synthetic wavelet-textures. *Vis. Res.* **41**, 585–598.
14. Dakin, S.C., Tibber, M., Greenwood, J.A., Kingdom, F.A.A., and Morgan, M.J. (2011). A common perceptual metric for human discrimination of number and density. *Proc. Nat. Acad. Sci. USA* **108**, 19552–19557.
15. Zavitt, E., and Baker, C.L. (2014). Higher order image structure enables boundary segmentation in the absence of luminance or contrast cues. *J. Vis.* **14**, 1–14.

Evo-Devo: Universal Toll Pass for the Extension Highway?

Qiyao Mao and Thomas Lecuit

Aix-Marseille Université, CNRS, IBDM UMR7288, Campus de Luminy, case 907. 13009, Marseille, France

Correspondence: thomas.lecuit@ibdm.univmed.fr

<http://dx.doi.org/10.1016/j.cub.2016.05.063>

The distinction between long-germ and short-germ insects is a classic one in evo-devo, yet a common genetic mechanism may underlie germband extension in all insects, even all arthropods.

When Gerhard Krause coined [1] (and Klaus Sander later elaborated [2]) the terms long-, intermediate- or short-germ to classify insect embryos, he was referring to the proportion of segments determined prior to gastrulation. Long-germ insects, such as the fruit fly

Drosophila melanogaster, specify most of their segments simultaneously at the blastoderm stage, before gastrulation partitions the ectoderm, mesoderm and endoderm. By contrast, short-germ insects start gastrulation with only a few segments, and then add segments more