How then might a terminal selector gene coordinate the expression of all neuronal features? Does this then mean that any terminal selector gene can also be proneural, and its role in terminal differentiation is merely a consequence of its temporal expression pattern? Terminal selector genes have been shown to act both early and late in the developmental progression of a given neuron type (e.g., [13]), suggesting that given the appropriate chromatin state, these and perhaps other developmental proteins may be more versatile than previously appreciated (although see below).

What is the reason for the apparent neuronal specificity of the reprogramming? One model is that LIN-53 may specifically function directly or indirectly in the repression of neuronal loci in germline chromatin. It is known that the REST transcription factor in mammalian differentiated non-neuronal cells or in stem cells recruits histone modifiers to convert neuronal loci to constitutive or facultative heterochromatin, respectively [14]. In this model, there would be similar factors that recruit specific modifiers and remodelers to subsets of tissue-specific loci in germline chromatin to act as gatekeepers of different differentiated states. Alternatively, there may be features of germ cells that facilitate conversion to neuronal cell types. For instance, it is possible that germline cells already express early proneural genes and that upon loss of *lin-53*, neuronal terminal differentiation genes are now accessible to terminal selector proteins.

Does this work lead us closer to direct conversion of any cell — and not just pluripotent or lineally related cells — into any other cell type *in vivo*? In some cases, misexpression of transcription factor(s) alone is sufficient to convert to a lineally unrelated cell fate [15–17], but in recalcitrant cases, this work suggests that a systematic exploration of chromatin-based inhibitory mechanisms may enhance directed reprogramming. The advantage of directed transdifferentiation as opposed to a program in which somatic cells dedifferentiate to a pluripotent state followed by redifferentiation to a specific fate [18] is a lower propensity for unregulated growth [19]. It is of course not yet known how these findings in *C. elegans* will translate more generally. It is also unknown whether the cells that are generated exhibit all properties of the endogenous cell type and whether they are fully functional. Nevertheless, these findings emphasize once again the importance of Waddington's epigenetic landscape [20], and highlight its dynamic nature.

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Visual Perception: More Than Meets the Eye

A recent study shows that objects changing in colour, luminance, size or shape appear to stop changing when they move. These and other compelling illusions provide tantalizing clues about the mechanisms and limitations of object analysis.

David Burr

Perception is deceptively effortless: we open our eyes and see a rich and dynamic world filled with wondrous colours and fine detail. However, we are periodically reminded that perception is actually not simple at

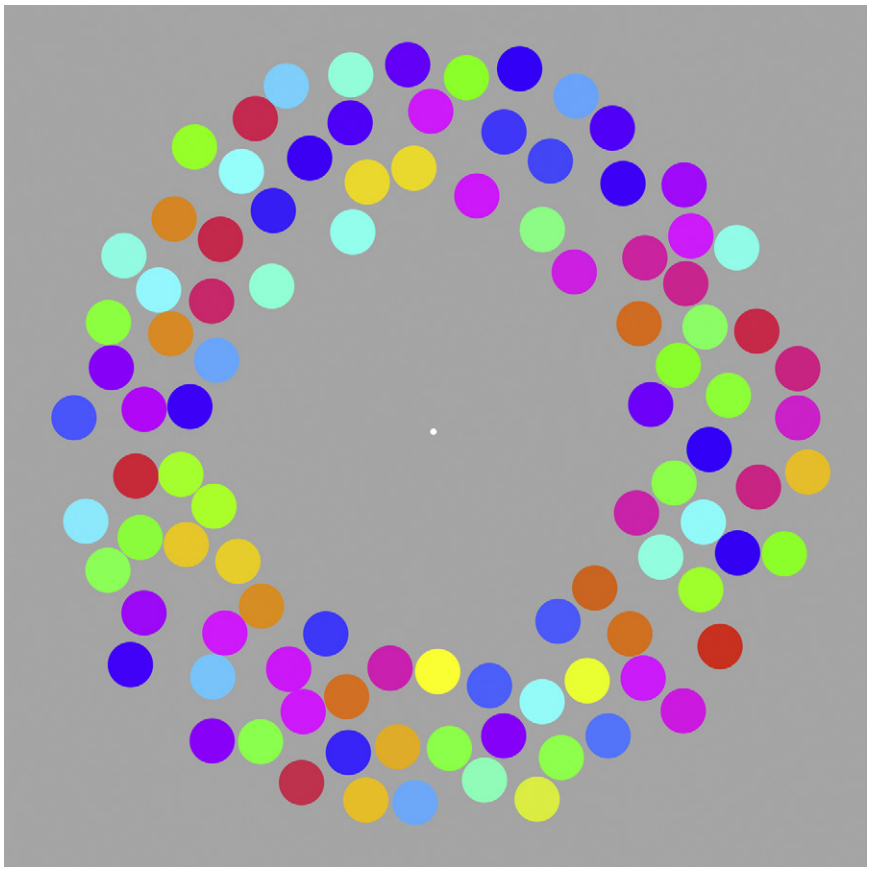

Figure 1. Illustration of the stimuli used in the Suchow and Alvarez [1] study.
Each dot changes continuously in hue. The changes are highly salient when the dots are stationary, but undetectable when the pattern is rotated about the centre.

all. One constant reminder is the abysmal failure of computer systems to mimic anything near our perceptual capacities (only recently can they read standardized number plates). But more intriguing are the dramatic perceptual illusions, such as one published recently in *Current Biology* [1]. The demonstrations reported by Suchow and Alvarez [1] are described in Figure 1, but readers should view them for themselves (the movies can be downloaded from http://www.cell.com/current-biology/abstract/S0960-9822(10)01650-7#suppinfo). Movie 1 shows a field of coloured dots, each continuously cycling through the colour spectrum; then all the dots begin to rotate around the fixation point — instantly the sense of individual change is lost, as each dot appears of fixed colour (although physically they continue to change). The other movies show the same effect with changes in luminance, size or shape: all these aspects remain defined, but no change is seen in the single dots. Clearly our perceptual systems do not report veridically, dot by dot, the events on the screen, but make an estimate, a summary statistic of the scene: lots of dots, lots of colours, and all in coherent motion. Information about the individual dots is lost: and we are completely unaware of this loss, even when attending to individual dots.

This is by no means the first demonstration that most detail in the world escapes our awareness. More than a decade ago, a couple of groups [2,3] devised stunning demonstrations of what has been coined 'change blindness' (demonstration movies can be seen at http://www2.psych.ubc.ca/~rensink/flicker/download/index.html). In the more popular version, two successive images of a scene are displayed, differing in a major feature — like the removal of an aeroplane engine! This change goes completely unnoticed if there is a flash between presentations (or a comparable trick such as using 'mud splashes' to mask the transient changes). Interestingly, attending to the region of the change (the aeroplane engine in the example mentioned) foils the effect, whereas the demonstration reported by Suchow and Alvarez [1] seems to resist attention to the individual dots. The discovery of change blindness actually has earlier roots in clever experiments which showed that image changes during saccadic eye movements go unnoticed [4].

Another, related demonstration was published in *Current Biology* a couple of years back ([5]; see http://www.pisavisionlab.org/CB_dispatch/demos.htm). Look at a field of many dots for a while, say 20 seconds, and then inspect a field with a moderate number: the number of dots seems dramatically reduced, to about half. Where do the missing dots go? And as the adaptation wears off and the apparent numerosity returns to normal, where do the dots return to? We always have the clear impression of seeing a precise number of dots in definite positions, but this must clearly be an illusion. The system seems to encode only rough statistics about quantity and distribution: adaptation affects the estimate of number, but this change is not perceptible at the level of individual dots.

Returning to the illusion under discussion, what does it tell us about vision (other than it is more complex than many believe)? Suchow and Alvarez [1] test the idea of 'temporal freezing' — introduced to explain another fine class of illusions [6] — by interrupting the moving display and flipping it to a past, future or present state. 'Flips' to the present were not noticed, while others were, suggesting to the authors that observers had in fact 'implicitly' updated their representation of the state of the dots, rather than 'frozen' the representation. While it certainly speaks against the 'freezing' hypothesis, this test does not prove that the system actually updates each dot. Abruptly stopping, then changing the display affects drastically the temporal characteristics of the display,

introducing a range of temporal frequencies not present in the rotating display. The same/different discrimination could be based solely on the transition of the stopped to the flipped image, without subjects having to 'update' anything.

My take on the demonstration is that it involves two processes, *global motion* and *crowding*. Motion perception is a complex task for vision, with conflicting requirements of integration and segregation. We know from physiology [7] and psychophysics [8] that some cortical neurons integrate motion signals over large and complex trajectories (including circular trajectories). It seems plausible that this integration process subsumes all the dynamic signals within the area, not only directional motion signals but also dynamic signals associated with changes in colour, size or shape. Yet another demonstration published in *Current Biology* ([9]; see http://www.pisavisionlab.org/CB_dispatch/demos.htm) gives a further example of complex-motion integration: dipoles oriented along a circular path, continuously refreshed in random positions, produce a strong sense of circular motion, although the stimulus contains no coherent motion signals. So strong and smooth is the sense of circular motion that it is hard to believe that the dipoles in fact appear and disappear at random. Even the mundane 'limited-life' motion stimuli used in many motion experiments show a similar effect (see http://www.pisavisionlab.org/CB_dispatch/demos.htm). Here individual dots move for a few frames along a coherent trajectory, to disappear and reappear in a new position. Again, observers are quite unaware of the births and deaths of individual dots; but when the dot-motion is halted, the twinkling of each dot becomes immediately apparent, and salient.

Suchow and Alvarez [1] conclude their report by emphasising the tight link between motion and object processing (often thought to be analysed separately). Having frequently hammered this point in these pages [10–12], I obviously agree. However, I believe that their demonstration in fact points to the limits of our capacity to analyse objects in motion. Spatiotemporal interpolation [13] enables the encoding of properties such as fine-scale vernier acuity, colour and shape for objects in motion [14,15], at least for single objects to which subjects attend. Suchow and Alvarez's [1] demonstration shows that this capacity fails for multiple objects packed too tightly for attentional mechanisms to operate: a limit of the conflicting requirements for motion integration and segmentation.

And this brings me to *crowding*, a term referring to the difficulty in reading peripherally displayed letters when embedded between others, although they are quite distinct when presented in isolation [16]. The phenomenon depends strongly on retinal eccentricity, and is not restricted to letters but generalizes to gratings, objects in general and even parts of faces (see [17] for demonstrations and discussion). Something similar may be happening here. Crowding does not increase with motion [18], but in Suchow and Alvarez's [1] demonstration the field of dots is already crowded, even when stationary, as the critical size for crowding is about half their retinal eccentricity (Bouma's Law [16]). Perhaps, when the display is not rotating, the dynamic change-signals of each element breaks through crowding, in the same way that temporal transients are known to cause 'pop-out', reaching awareness without active attention [19]. If the change-signals are subsumed by global motion mechanisms, we are left with a field of crowded objects of different size or shape or colour, without precise knowledge of which individual dot has which colour. Relating Suchow and Alvarez's [1] demonstration to crowding could be useful, as crowding is a well-studied field, with well-defined laws and firm hypotheses about its neural basis [17]. For example, the crowding explanation predicts Bouma Law behaviour: 'motion silencing' should occur only when the elements fall within a critical region, whose size increases directly with retinal eccentricity. This is a simple hypothesis to test.

Like many stunning visual demonstrations, this one will probably raise more questions than it answers, and is certain to spark a lively debate. But whatever their explanation, these clever demonstrations show yet again that there is more to vision than meets the eye. Visual perception does not work solely by analysing the signals emanating from the retina, but is active, constructing something akin to what the late Richard Gregory termed *perceptual hypotheses* [20]: and when these hypotheses are not perfectly matched with reality they can give rise to startling illusions.

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