

appears to be an important precondition that enabled the compartmentalization of one of the channels in the electric organ, allowing positive selection on the gene for that channel. This occurred not once, but twice — once in mormyrids and once in gymnotids. Is it a stroke of luck, or are such gene duplication events gateways that allow selection to operate with fewer constraints?

A similar situation occurred in the evolution of long-wavelength opsins in insects [17], where a gene duplication event seems to have facilitated the evolution of an opsin that is sensitive to red light [18]. Homology mapping suggests that a phenylalanine to tyrosine substitution at amino acid 139 of the green opsin occurred independently at least twice in butterflies and twice in bees, resulting in the repeated appearance of a red-shifted opsin [19]. In this example, therefore, the same amino acid substitution occurred independently at least four different times. This is not just a coincidence; it is an inherent physical property of the opsin that this particular amino acid substitution will result in a red shift. Computational models of selection suggest that, if a specific amino acid substitution is beneficial, then it is more than twice as likely to occur repeatedly than if the change is neutral [20]. Therefore, it is not a fluke that the same amino acid substitution occurred repeatedly; gene duplication and the inherent properties of the opsin facilitate this occurrence.

When we look at the remarkable similarities that arise through convergent evolution, such as in the electric organs in African mormyrids and South American gymnotids, we should not just dismiss them as amazing coincidences. Rather, they show that there are some paths that are more easily taken in evolution, allowing disparate organisms to converge on the same destination. Furthermore, these studies show that when selection repeatedly acts on certain parts of a protein, it indicates that those regions have functional significance. Thus,

studying the evolutionary variation in a structure can lead to a greater understanding of the basic properties of that structure.

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Visual Physiology: Perceived Size Looms Large

Visual illusions tell us that size perception depends heavily upon complex contextual cues, often thought to be extracted by brain areas high in the visual hierarchy. Now, a new study shows that perceived size is reflected in activity as early as the primary visual cortex.

Sean P. MacEvoy and David Fitzpatrick

Ask any fledgling artist how to make one object appear farther away than another, and you will likely get the same answer: draw it smaller. It is a simple consequence of the geometry of the eye — or of any pinhole camera — that the size

of an image formed by an object shrinks in proportion to its distance from the observer. **Figure 1** shows what happens if an object's size is not scaled appropriately to its distance; the 'distant' sphere appears larger than the foreground sphere, even though the two have the same physical dimensions (get a ruler and test it) [1]. This is

a classic size illusion, bane of grammar school artists everywhere, but long appreciated for its illustration of the powerful influence of context on our perception of the visual world.

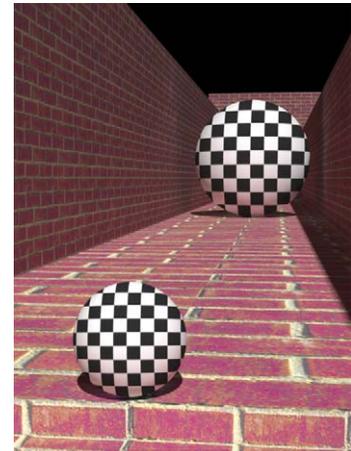
But where and how do illusions of this sort arise within the brain? It is a question that has bedeviled philosophers and biologists for centuries, and is particularly thorny in the case of the size illusion. The effect shown in Figure 1 depends upon linear perspective and a host of other depth cues, such as shading and occlusion, coupled to our own expectations of how big the spheres 'should' appear, given their distances. It has been fair to surmise that the size illusion emerges from some brain area where these perceptual and cognitive factors emerge, presumably high in the visual hierarchy and not in early visual areas that are seemingly devoted to maintaining a precise representation of visual space. In a newly published study, however, Murray *et al.* [1] present striking evidence to the contrary: using functional magnetic resonance imaging (fMRI), these authors found that they could detect the neural signature of the size illusion as early as the primary visual cortex (V1).

Employing tricks of perspective long used by artists to convey depth on canvas, Murray *et al.* [1] had subjects view a two-dimensional electronic rendering of a brick hallway receding into the distance (Figure 1). At both the 'near' and 'far' ends of the hallway, the authors inserted identical spheres. Even though these spheres had the same physical size on the screen, their position within the scene led subjects to judge the far sphere to be about 20% larger — a manifestation of the size illusion. Next, subjects viewed the same scene in an MRI scanner while staring at the center of either the near or far spheres. Surprisingly, larger regions of subjects' primary visual areas were activated by the far sphere than by the near sphere, even though the angular size of both was identical.

Of course, one could argue that the spheres differ in other respects,

such as their immediate surroundings, and perhaps the change in scale of cortical activation is a reflection of these differences, rather than a neural correlate of perceived size. To address this confound, Murray *et al.* [1] compared the differences in cortical activation resulting from the size illusion to those evoked by spheres that truly differed in size. If the different areas of activation produced by the spheres in the size illusion were due to their perceived size, rather than other aspects of the scene, one would expect to observe the same pattern for true size differences matched to the magnitude of the illusion. They found that this prediction held up: true differences in size evoked changes in the scale of cortical activation that were virtually indistinguishable for those evoked by illusory size differences. Moreover, they found that they could predict the magnitude of illusory size differences from fMRI data under conditions that altered the perceptual effect. Most impressively, they were even able to use their fMRI results to predict twists on the size illusion that had not previously been appreciated.

While these results certainly provide new insight into the neural basis of the size illusion, the biggest surprise is what they reveal about the functional hierarchy of the visual system and the role of V1 in particular. One of the hallmarks of early visual areas such as V1 is their preservation of the fine scale structure of retinal topography [2–4]. Retinal ganglion cells send their axons to the lateral geniculate nucleus (LGN) of the thalamus, which in turn provides input to V1. At each of these stages, the spatial arrangements of inputs are preserved, such that retinal space is mapped with exquisite precision in the cortex. As a consequence, conventional wisdom assumes that when two objects, viewed at the same eccentricity, occupy the same retinal area, they will activate the same amount of V1. By refuting this assumption, the evidence from Murray *et al.* [1] tells us that activity in V1 may have much to do with representing the dimensions that objects are expected to have, given



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Figure 1. The size illusion.

Although the two spheres have the same diameter, we perceive the 'distant' sphere to be larger. (Reproduced with permission from [1].)

their distance, as it does the simple projection of light they cast upon the retina.

This result also highlights the dynamic nature of V1 organization. To appreciate this, consider a cortical neuron just outside the region activated by an isolated sphere, here approximated by a disk, devoid of any context (Figure 2). Retinotopy dictates that a response is evoked only when the image of the sphere falls on the portion of the retina from which the neuron receives input, called its receptive field. Its inactivity is testament to the absence of appropriate visual stimulation from its receptive field. According to the results of Murray *et al.* [1], when the sphere is placed in a context that makes it look larger, this cortical neuron becomes active, even though the dimensions of the sphere are the same. As the retinal image has not changed, we are left to infer that the receptive field itself has moved on the retina to a location inside the boundaries of the retinal stimulus. Conversely, when a neuron stops responding to a sphere placed in a context that makes it look smaller, we can infer that its receptive field has swung outside the retinal image of the stimulus. In the context of millions of neurons across several millimeters of cortex, the rearrangement amounts to a dynamic redrawing of the map of visual space.

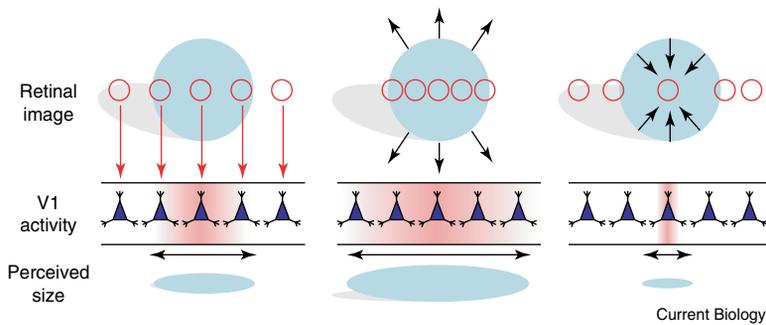


Figure 2. Dynamic remapping of visual space in V1 with changes in perceived size. Viewed in isolation (left column), the blue disk evokes activity among the set of V1 neurons whose receptive fields (red circles) cover the image it forms on the retina. When the same object is viewed in a context that makes it appear larger, the area of V1 activation grows (middle column). As V1 is organized retinotopically, this suggests that the receptive fields of previously inactive neurons have shifted to cover the object. Similarly, when the object appears smaller, receptive fields must have moved outside it (right column).

Similar fast reorganization has been encountered before. Shifts in receptive field location have been seen in ‘higher’ visual areas, such as V3 or V4, in conjunction with eye or stimulus movements, although these changes have typically been very brief [5–7]. While fMRI cannot tell us much about the time course of the remapping observed by Murray *et al.* [1], if the persistence of the size illusion is any clue, its duration is likely long. In V1, a few studies have noted that the size and locations of V1 receptive fields can change depending upon the contents of the receptive field, or even of surrounding areas [8–10]. Although these phenomena have lacked a clear perceptual link, scaled up to the population level they could produce shifts similar to those observed by Murray *et al.* [1]. Together, these findings contribute to a growing body of evidence for the capacity of the visual system to adjust quickly to demands placed by changes in either the environment or behavior [11,12].

The results of Murray *et al.* [1] underscore the power of feedback mechanisms in this process. Although some neurons in V1 are sensitive to real depth differences [13], there is little doubt that the ability of V1 to register size in a two-dimensional image results from the extraction of cues beyond its power to resolve. Appropriately, V1 sits within a complex network of visual areas and receives feedback from regions that have been implicated in the perception of

shape and depth, as well as the allocation of attention [14,15]. The adaptive advantage of this arrangement is in the flexibility it affords: the brain can use feedback to set V1 to the optimal configuration for the perceptual task at hand, as an alternative to maintaining multiple costly areas with narrow computational specialties.

An open question is: how far we can take these results? Do other illusions of size — including the familiar Muller-Lyer and the maddening Jastrow illusions — leave their marks on V1? What about size constancy, our useful ability to consistently judge an object’s size even as its distance changes? Also, implicit in this discussion is the idea that the perceived size of an object is ‘read out’ from the amount of cortical space occupied by its representation. Strictly speaking, this cannot be uniformly true: because the amount of cortical area devoted to a given point on the retina shrinks with eccentricity, an object moving from the center of gaze to the periphery will occupy progressively less cortical territory even though its perceived size remains constant. A simple space code was sufficient to recover perceived size under the controlled conditions used by Murray *et al.* [1] In real-world situations the problem is considerably more complex. Future experiments will be necessary to clarify these and other issues; the size story still has

a lot left to be written. Still, thanks to Murray *et al.* [1], the role of V1 will not be overlooked.

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