break formation [12] and could act as a signaling mechanism. It will be interesting to see whether checkpoint kinase activation can trigger synapsis initiation at centromeres.

Another obvious question concerns the importance of this coupling mechanism. Indeed, although the coupling of synapsis to chromosome fragmentation is widely conserved, it is not a general phenomenon, and a number of organisms, including flies and nematodes, undergo meiosis successfully without this additional level of control [1,3]. A possible clue lies in the fact that synaptonemal complex formation does not *a priori* occur between homologous chromosomes. Non-homologous synapsis is observed in a variety of situations where homology search is impeded or impossible, including inversion heterozygotes and haploids [3]. Thus, meiotic cells need mechanisms to ensure that synapsis only initiates between homologous chromosomes. Interestingly, in budding yeast and mice, where coupling of synapsis and chromosome fragmentation is observed [3,6], the exposed chromosome breaks provide the primary means to identify homology and align matching homologous chromosomes [16]. In contrast, flies and nematodes are highly proficient in homolog alignment even without chromosome fragmentation [16,17]. In flies, homologous chromosomes are aligned not only in the germ cells, but also in practically all somatic cells of the adult organism [17]. Nematodes, on the other hand, have chromosome-specific pairing centers at the ends of all chromosomes that identify homologous chromosomes in the absence of chromosome fragmentation [9,16]. Hence, an intriguing correlation emerges, whereby organisms that require chromosome breaks for homology search couple synapsis initiation to break formation, whereas organisms with break-independent pairing mechanisms do not.

Finally, if coupling synapsis initiation to chromosome fragmentation is so important in budding yeast, why not dispense with centromeric initiation sites altogether and make chromosome breaks the exclusive nucleation sites? It is possible that centromeres provide a backup mechanism. Because every chromosome has a centromere, this setup would ensure synapsis on chromosomes that failed to undergo chromosome fragmentation. In this context it is worth noting that even in the absence of synaptonemal complex zippering, the presence of synaptonemal complex components at centromeres is sufficient to tether pairs of centromeres together [18]. Although this coupling is non-homologous, it may assist with the correct alignment of individual pairs of homologous chromosomes, for which homology search failed.

Clearly, the current work has raised many new and intriguing questions and is bound to inspire further investigations into the complexities of synapsis.

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Vision: Thinking Globally, Acting Locally

The global structure of images profoundly influences how we see their local detail, consistent with activity in primary visual cortex being *disambiguated* via feedback from later visual areas.

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In this issue of *Current Biology*, Warren and Rushton [1] describe how the direction in which we see objects move can be strongly influenced by movement of the surrounding scene, in a manner that is consistent with the brain attempting to discount the disruptive influence of our own movement. This suggests that known neural mechanisms sensitive to *optic flow* — the patterns of visual motion that arise under self-motion — may be
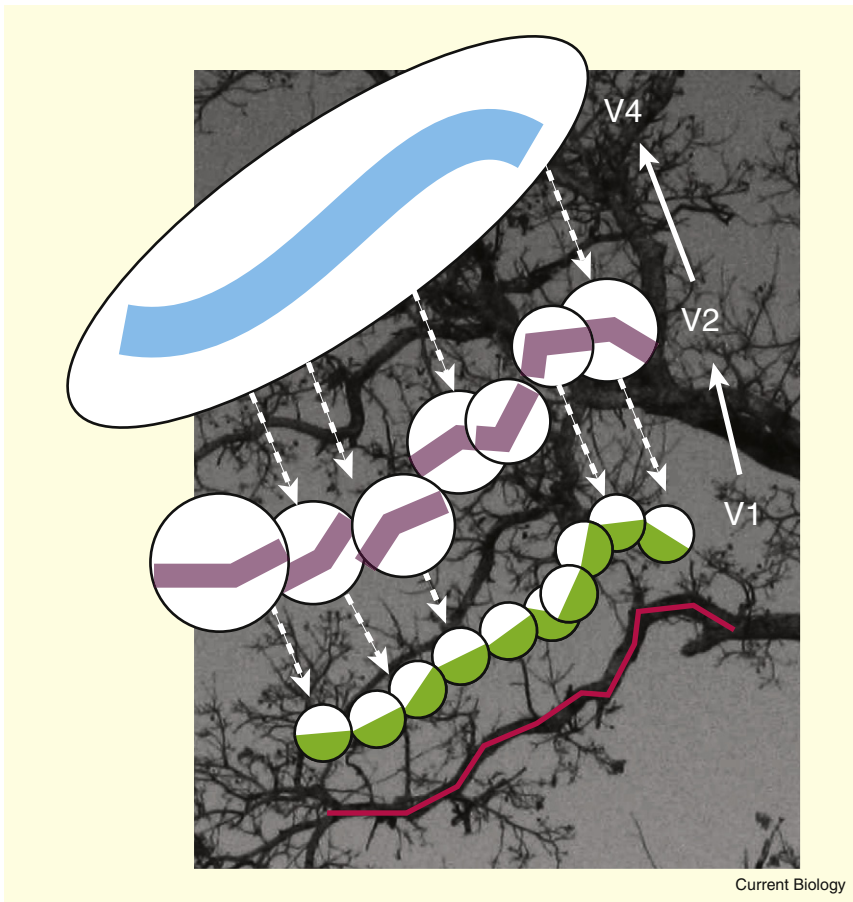
Figure 1. Shape representation in visual cortex.
Representation of shape in the visual cortical hierarchy involves feed-forward connections (solid arrows) between areas representing increasingly complex features, as well as feedback connections (dashed arrows) onto preceding areas.

used not for navigation but to provide a 'calibration signal' that helps maintain a correct sense of object-motions within a moving environment. Although it has long been known that the visual context that objects arise in affects their appearance, Warren and Rushton's [1] report that the effective visual context can be far from the object itself is representative of a more recent trend in psychophysical research indicating that *neural feedback* must play a central role in how context exerts its influence.

Arguably the single most important concept underlying our understanding of vision is that neurons in the visual pathway — retina to lateral geniculate nucleus (LGN) to cortex — selectively respond to features falling within an area of visual space known as their *receptive field* [2]. Although a simplification — for example, visual

neurons are not independent and are frequently suppressed by the activity of their neighbors [3] — this concept has had an enormous influence on our understanding of vision. As one moves through the visual pathway, the structure that neurons respond to becomes more complex (Figure 1): while cells in the retina/LGN prefer spots of light [4], in V1 they respond to lines [5], in V2 there is preference for corners [6], in V4 it is for outline-shapes [7] and so on.

This increase in complexity of preferred-stimuli is consistent with cells at each stage refining the selectivity of their input stage, promoting a view that the visual system is predominantly *feed-forward* where selectivity at each stage is derived by combining input from the preceding stages. This combination can be achieved by the operation of receptive fields, or interactions between neurons,

but essentially it occurs within a given stage. That said, physiologists and anatomists have long reported the presence of connectivity that supports not only feed-forward but also *feedback* activity in the visual system (for review see [8]). A surprising example is that cells in the LGN — frequently characterized in textbooks as little more than a relay for retinal-signals *en route* to the cortex — receive around three times as much input from feedback from V1 as they do from retinal afferents [9].

As one proceeds along the visual pathway, receptive fields not only increase their complexity but also grow in size and decreasingly care about the specific location of their stimulus in the visual field (for example [10]). Consequently their ability to encode the position of objects will become increasingly poor. Because V1 generates a dense and spatially precise description of the world, why throw that away and generate a new strictly retinotopic representaton in each subsequent area? An emerging alternative view is that we might reuse V1 by performing complex computations, for example of shape, and then feeding that information back onto V1 to disambiguate and bind local orientation information.

In the case of contour information, for example, elegant anatomical work has shown that the range of connectivity in V1 cannot support binding of remote orientation-tuned receptive fields across space, but that feedback from later visual areas can [11]. Figure 1 illustrates this example. Overlapping receptive fields in V1 (green/white) could represent dense local orientation structure of the contour highlighted in red, but horizontal connectivity in V1 is insufficient to support binding of local orientation into global shape information. Instead, if more complex features of the contour, such as corners, shape, and so on, were processed via feedforward connectivity (solid lines) in, for example, V2 and V4, then these areas could sacrifice retinotopic precision, and then regain it by feeding signals back onto their input areas. Such modifications would serve to bind remote signals, overcome noise, etc. Indeed Sillito

and colleagues [8] have provided compelling evidence that responses in motion selective area MT in the macaque can influence activity in primary visual areas and even the LGN, in a manner which is consistent with them refining their spatial and temporal tuning properties, for example to support predictive encoding.

In terms of human visual behaviour, it has long been known that the global structure of images can influence the appearance of the local features of which they are composed; indeed, this is the basis of virtually all visual illusions. Figure 2A shows two versions of the same image; each is a contrast- and orientation-flipped version of the other. The presence of the face in the rightmost image completely changes how we see the ink-blobs (for example, some now appear to be shadows). This is a relatively high-level effect on appearance, but global influence can also affect more low-level spatial properties, such as *crowding* (the tendency of nearby clutter to interfere with our ability to recognize objects in the peripheral visual field).

Figure 2B illustrates the phenomenon. While fixating on the red "1" the orientation of the central element of the leftmost stack of ellipses is hard to determine. A variety of evidence indicates that, although crowding can be influenced by high-level factors such as attention, it does not reflect a limitation of such processing but rather of cortical resources in early visual areas [12]. Because crowding happens when objects are too close together it is natural that much research has focused on determining the critical spacing between one object and another before crowding arises, i.e. determining the local interactions that determine crowding. Fixating "2" in Figure 2B illustrates that the central element may be slightly easier to see now the elements have been pulled apart. The third part of Figure 2B, however, shows that local structure is not always the primary determinant of crowding. Fixating the "3", it is easy to see the orientation of the central element even though the target is the same distance from its nearest flank as in "2". These and other findings like it [13] indicate that it is the global

organisation of the pattern that determines crowding, and it has been suggested that crowding may serve to regularize a noisy local representation of the visual world in

line with the statistics of our visual world [14].

The lower part of Figure 2 gives two examples of how global motion-structure can influence our perception
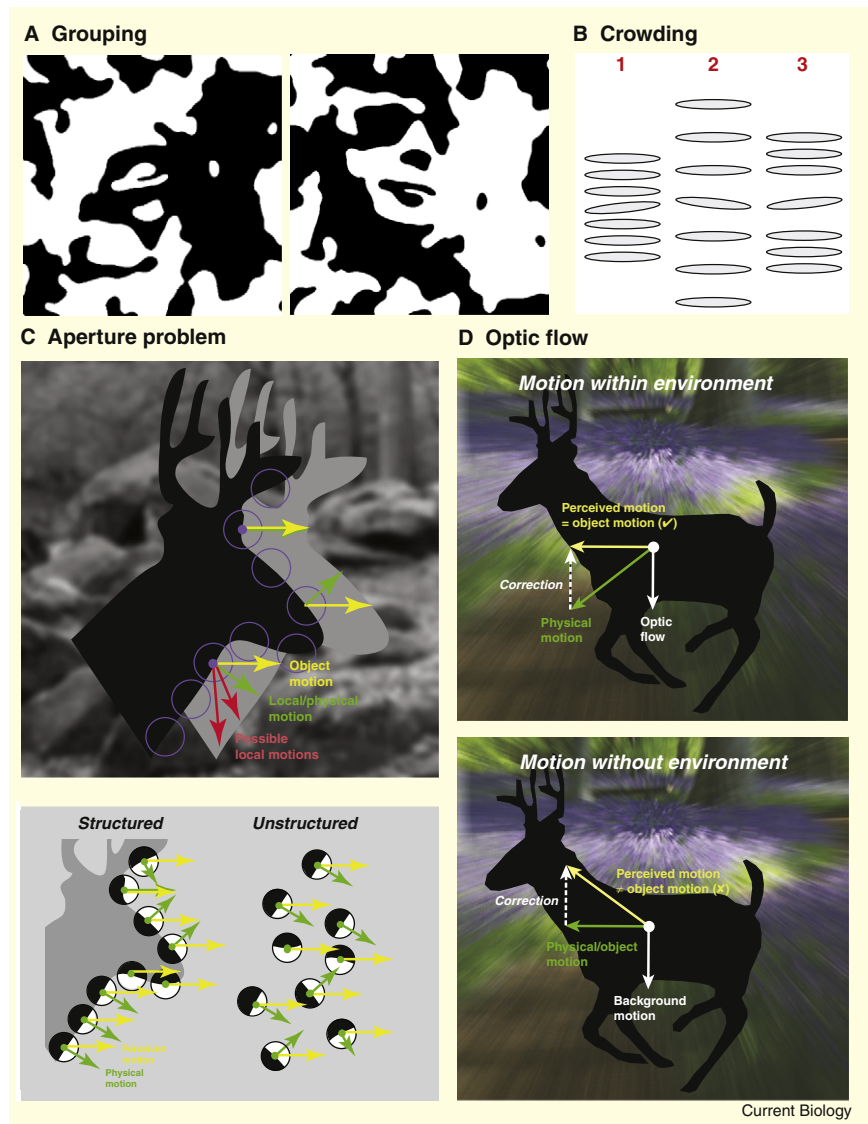

Figure 2. Examples of how global structure influences how we perceive an image's local structure.

(A) The presence of the face in the right part of the figure changes ink-blobs into shadows. (B) While looking at the red "1" the tilt of the central ellipse in the stack below is unclear due to *crowding* from its neighbours. Increasing element separation helps a little (fixate "2") but fixating "3", the orientation of the target is easy to see even though neighbor-separation is identical to "2". Global organization relieves crowding. (C) The local motion arising from extended contours is ambiguous because motion-responsive neurons only encode directions perpendicular to their preferred orientation, requiring that local motion be pooled across space. Two recent studies [17,18] have shown that the binding of such information is not linked to contours; scrambling the location of essentially randomly oriented lines whose speeds are consistent with the movement of an underlying object elicits a compelling percept of rigid motion, and of all elements moving at a common velocity. (D) Warren and Rushton [1] report that we correctly judge object motion by subtracting the contaminating motion cues arising from our own movement (top). This can explain errors in judging direction of motion when objects translate in front of optic flow (bottom), and suggests that cortical mechanisms dealing with optic flow may be there principally to help us ignore it.

of local motion. Figure 2C illustrates that motion-responsive neurons in early visual areas, such as V1, respond strongly to motion of contours at their preferred orientation. Consequently they only encode information about motion *perpendicular* to their preferred orientation (green arrows). When the edge of an object passes through a series of V1 neurons' receptive fields (purple rings) it produces an ambiguous pattern of motion that is consistent with many contour-directions and speeds (red arrows) as well as the true contour motion (yellow arrows). This is the *aperture problem* for motion; solving it requires binding of motion across space. Until recently this was widely believed to be solved in area MT — which has large motion-selective receptive fields suitable for pooling — based on findings that neurons in this area can correctly encode the global direction of plaid stimuli (composed of two superimposed gratings) [15]. A recent electrophysiological study [16], however, has shown that this computation breaks down when the two orientation-components of the plaid are presented to two different (but responsive) parts of an MT neuron's receptive field. This indicates that the aperture problem has been solved on a more local basis before signals reach MT when responses may be further disambiguated using feedback from later visual areas.

Recent psychophysical studies [17,18] have also probed the nature of local-disambiguation of object motion. Presenting a series of moving contours behind apertures (Figure 2C, *Structured*), where the local speed/ direction/position cues are consistent with the motion of a rigid object, leads to a compelling percept of rigid motion, where all the local elements appear to move in concert with a common velocity. Scrambling the positions of the same elements (Figure 2C, *Unstructured*) produces a field of essentially randomly-oriented contours which, remarkably, still elicits a strong sense of global motion and a sense that local elements are moving at the same velocity. This indicates that the visual system does not use object shape, but only the combinations of speeds/directions that are present to disambiguate local motion [17,18], and more generally that

global cues to motion can override local cues. Amano *et al.* [17] went further and showed that the disambiguation strategy employed in human vision is adaptive, switching (as required) between global pooling of ambiguous contour motion across space (as we have seen) to more local pooling of unambiguous motion signals. The solution to the aperture problem is thus a complex trade-off between local and global motion information, whose end-result is manifest in our representation of both.

Warren and Rushton [1] describe another way that global organization can profoundly affect our perception of local motion structure (Figure 2D). Our own movement generates optic flow that contaminates motion cues arising from objects. We are largely unaware of this, perceiving object motion veridically under natural viewing conditions, and the authors propose that this tolerance could arise from our subtracting out the local 'optic flow' signal to compensate for our own movement. Consistent with this view, Bartels *et al.* [19] showed observers feature movies and report that the response of their early visual areas (assessed using functional magnetic resonance imaging) correlated well with the residual motion signal (derived by subtracting global motion from the flow field). A downside of this strategy is that we over-apply it; objects that translate in front of (rather than within) a moving environment appear to move in the wrong direction. These errors are predictable, and the compensatory signal must arise from global information (and not from local interactions between motion sensors responding to the object and its surround) since such errors arise even when optic flow and object are remote from one another [1]. The idea of flow-subtraction is not uncontroversial given the traditional view that the purpose of optic flow processing — and the considerable cortical resources supporting it — is to help us navigate [20]. Instead we are faced with the prospect that our sensitivity to optic flow may stem from the way in which we choose to ignore it; a global motion processor feeding signals back to its own input areas in order to disambiguate local information.

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