Figure 1. The ant *Formica fusca* collecting honeydew from nymphs of the treehopper, *Publilia concava* (photo courtesy of Manuel Morales).

ant host's brood odour such that they are carried to the ant's nest where they then predate ant brood [9]. Sensory traps are common in mutualisms, whilst cost-enforced honest signalling is relatively rare, which contrasts with the ubiquity of honest signals employed in mate selection and predator deterrence [8]. Cost-enforced honest signalling has only been demonstrated in plant–pollinator systems. It may be that partners in many mutualisms have limited recourse to sanctions that might punish bad behaviour by their partners [8,10].

It is easy to see how the coercive, dishonest signalling employed by lepidopteran mutualists could switch to greater exploitation and parasitism. However, the honest by-product mutualism between aphids and ants also becomes exploitative when environmental conditions change. For example, when an alternative, superior carbohydrate source is made available ants prefer to predate aphids rather than harvest honeydew [11].

Morales *et al.* [6] have provided a valuable insight into the role of communication in mutualisms. Alarm signalling by treehoppers clearly increases the coordination of benefits with ants, and this may be especially important when high population density means there is competition for ant services. In contrast, the coercive means employed by lepidopteran caterpillars might improve their prospects of receiving protection, especially when they have inferior rewards on offer compared to constitutive honeydew producers. This subtle analysis of differences in interspecific interactions confirms a key role for communication in coordinating the investments partners make in mutualisms.

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Imagery: Mental Pictures Disrupt Perceptual Rivalry

Are mental images like pictures? Yes, according to a new study showing that imagery can have a high degree of visual specificity and thereby disrupt perceptual rivalry.

Scott D. Slotnick

It has been debated for centuries whether visual mental imagery is pictorial or symbolic, like language (Figure 1, left and center). A growing body of neural evidence has recently weighed into the debate, capitalizing on the hierarchical nature of visual cortical processing [1,2] where simple visual features, such as line orientation, are processed in posterior occipital regions and increasingly abstract information is processed later in the occipital-temporal processing stream (Figure 1, right). Specifically, there is evidence suggesting imagery can be pictorial as this mental process can produce activity in early visual regions [3] and has even been shown to evoke activity with topographic organization reflecting the precise stimulus location in the visual field [4–6]. A sound argument can be made, however, that such activity does not reflect a core aspect of the imagery *per se*, but is rather epiphenomenal (like the noise given off by a car engine). A recent *Current Biology* paper by Pearson *et al.* [7] reports that visual imagery can disrupt binocular/perceptual rivalry. This is the most compelling evidence to date that imagery can be pictorial.

Binocular rivalry occurs when a unique stimulus is presented to each eye but only one stimulus is perceived (dominant) at any given time, as if the stimuli compete for access to consciousness. In the Pearson *et al.* study [7], green vertical gratings/lines and red horizontal gratings/lines were briefly presented to the left and right eye, respectively, and then, after an intervening period, the same patterns were again briefly presented. For each rivalry display, participants reported the stimulus they perceived (vertical or horizontal gratings). When participants passively viewed the display, their perception was quite stable across the first and second presentation (80% of

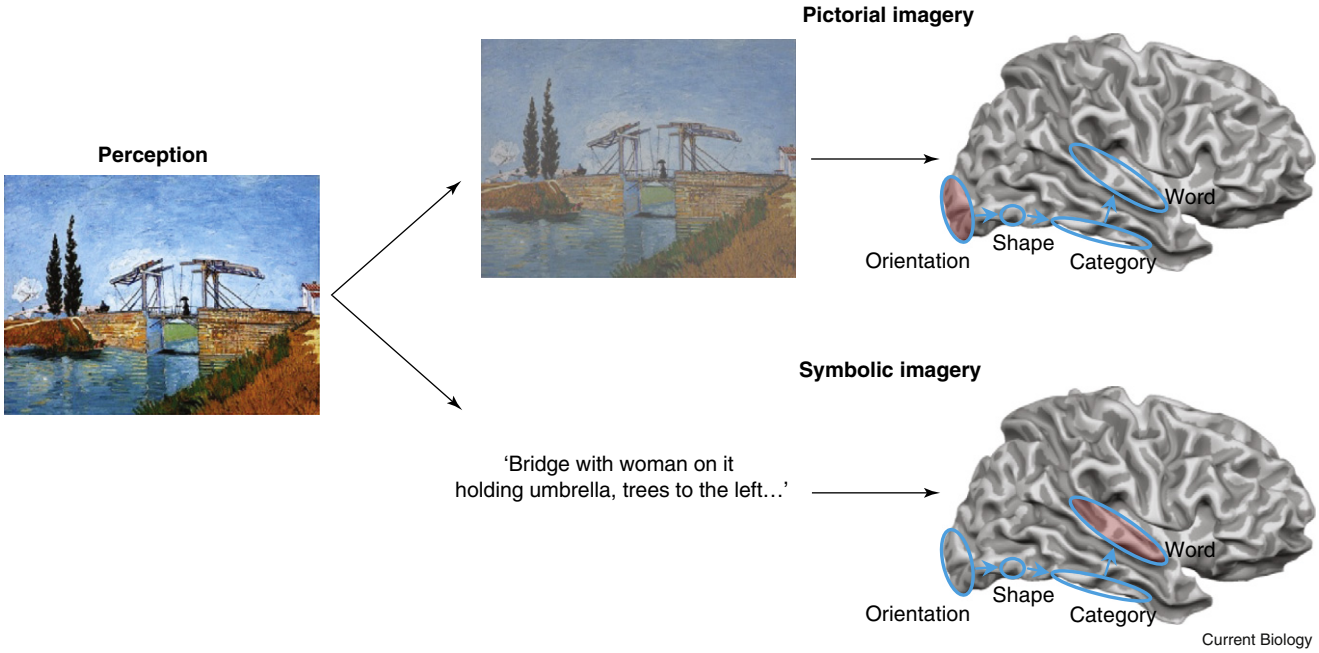

Figure 1. Visual imagery: pictorial or symbolic?

What would you experience if you studied the painting by van Gogh to the left (Cologne: Wallraf-Richartz Museum) and then imagined it? Some believe the image can be pictorial, having a similar type of visual representation as the perceived painting (but with reduced intensity, as shown in the upper center panel), while others argue that the image is represented symbolically (such as a verbal description, as shown in the lower center panel). One way to distinguish between these hypotheses is to evaluate the predicted pattern of brain activity corresponding to the known hierarchical organization of visual cortical processing. The simplest visual features (such as line orientation) are processed in the posterior occipital cortex with progressively more abstract processing (object shape, category, and ultimately the verbal label/word) occurring later in the occipital-temporal processing stream (neural regions associated with each type of processing are demarcated by ovals, with successive stages connected by arrows). If imagery is pictorial, it should activate visual processing regions (as shown in the upper right panel, red shading), while if imagery is symbolic is should activate word processing regions (and not visual processing regions, as shown in the lower right panel).

the time the same stimulus was dominant for both presentations, where 50% corresponds to a chance level of perceptual stability with an equal probability of perceiving either stimulus on the second presentation). When participants imagined the non-dominant stimulus during the intervening period — for example, a horizontal grating if a vertical grating had been perceived during the first presentation — it lowered perceptual stability between the first and second presentation to chance levels.

Pearson *et al.* [7] then assessed the degree to which imagery might reflect weak perception by presenting a non-dominant stimulus in the intervening period (rather than having participants imagine it) and varying the level of stimulus intensity. At 40% intensity, the perceptual effects mirrored the imagery effects (bringing the perceptual stability to chance levels, with a similar effect also observed by reducing stimulus contrast). Furthermore, systematically increasing the temporal duration of perception (at reduced intensity) or imagery of the non-dominant stimulus during the intervening period systematically reduced perceptual stability. These results were very similar for the perception and imagery conditions, suggesting that imagery can be pictorial and equivalent to a perceptual stimulus at reduced intensity.

In a final experiment, Pearson *et al.* [7] measured the degree to which these effects corresponded to the specific orientation that was perceived or imagined. The protocol included just two stimulus presentations (like the passive viewing condition described above). The first presentation was either a green vertical grating or a red horizontal grating in the perception condition (at 40% intensity), or a cue to imagine one or the other of these stimuli in the imagery condition (keep in mind that only one stimulus was perceived or imagined in the first presentation, so there was no rivalry). The second presentation included the rivalry pair as described previously (referred to as 0 degree orientation difference, as one of the stimuli had the same grating orientation as the first presentation) in addition to rivalry pairs with other orientations. Perceptual stability between the first and second presentations was used to systematically measure orientation effects. An orientation difference of 0 degrees resulted in a high degree of perceptual stability (replicating the passive viewing condition results above), an orientation difference of 22.5 degrees produced less perceptual stability, and a difference of 45 degrees yielded chance levels of perceptual stability. These effects were remarkably similar for both perception and imagery and provided further evidence that imagery is akin to perception with reduced intensity. Of additional importance, these results show that imagery can contain orientation specific information which limits the candidate neural regions that might underlie these effects.

Only early visual regions — such as V1, V2, V3, V4 or V8 — have a topographic representation of space, with neighboring regions of the visual field mapped onto neighboring regions of cortex [8–10]. Within these regions,

the visual representation can be described as truly pictorial. Moreover, only the first few visual regions (V1, V2 and V3) are orientation selective, with sub-regions that process specific stimulus orientations [11,12]. It is therefore not surprising that binocular rivalry studies that have used orientation grating stimuli have reported modulation of activity in these orientation-selective regions [13,14]. It follows that the binocular rivalry stimuli used in the new study by Pearson *et al.* [7] also evoked activity in these regions. When considered in conjunction with the observed orientation specific effects of imagery, the evidence suggests the interactions between imagery and perceptual rivalry occurred within the earliest orientation selective visual regions.

Evidence bearing on the depictive nature of imagery can be broadly classified as either correlational or disruptive. Correlational evidence, which is abundant, refers to imagery effects that mirror perception and includes behavioral findings — such as shifting attention between objects in an imagined visual scene takes progressively longer as distance increases, as if the image is being scanned [15] — and neural findings (mentioned previously). Such evidence could be disregarded by symbolic imagery theorists as epiphenomenal, however, because it is possible that it reflects mental operations that have nothing to do with imagery — for example, a mental simulation based on knowledge that symbolic imagery might follow known physical laws, such as it takes longer to scan greater distances [16].

Disruptive evidence refers to interference of a given mental process either by another process that shares the same neural substrates or by direct disruption of the underlying neural substrates. Such evidence supporting pictorial imagery is relatively sparse. Behavioral work has shown imagined vertical lines can impair performance on a perceptual line discrimination task [17], a patient's imagined (and perceived) visual field was restricted following partial removal of occipital cortex [18], and temporary cortical deactivation of occipital cortex impaired performance on a task involving imagery of oriented lines [19]. This type of evidence is particularly convincing because it shows visual perceptual processing or visual processing regions are necessary for imagery.

The new study by Pearson *et al.* [7] provides a much needed contribution to the category of disruptive evidence. They showed that imagery disrupted binocular rivalry in an orientation-specific manner, suggesting orientation processing in early visual regions was necessary for both perception and imagery. It is notable that even if this evidence was correlational, it would still be impenetrable to a mental simulation argument (as it would be nonsensical to propose participants had any knowledge of how rivalrous perceptual stimuli and imagined stimuli might interact). Considering these factors, this evidence can be considered the most compelling to date that imagery can be pictorial.

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Microtubule Stabilization: Formins Assert Their Independence

Mammalian Diaphanous-related (mDia) formins are well known for their actin nucleation and filament elongation activities. They have since emerged as microtubule-binding proteins, and a recent study shows that mDia2 stabilizes microtubules independently of its actin nucleation activity.

Aaron D. DeWard and Arthur S. Alberts

Side by side, microtubules and filamentous actin (F-actin) work in concert to facilitate essential changes in cell morphology [1,2]. One mechanism governing actin remodeling includes Rho GTP-binding proteins signaling through mDia formin