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Department of Plant Sciences,
University of Oxford, South Parks Road,
Oxford OX1 3RB, UK.

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Action Perception: Seeing the World through a Moving Body

Recent evidence suggests that the acquisition of new motor skills can directly influence later visual perception even when an observer's eyes remain 'wide shut' during learning.

Ian M. Thornton¹ and
Günther Knoblich²

Functionally, there can be little doubt that perception and action are tightly coupled. In order to survive, animals must be able to detect dangerous or desirable stimuli in the environment so that they can plan and execute appropriate avoidance or approach behaviours. Often, such planned actions must also be adjusted mid-movement under the guidance of perceptual input to account for ongoing environmental change. Still a topic of much debate, however, is exactly how such action-perception coordination is accomplished. More specifically, the exact relationship between the underlying representational and neural substrates of these systems remains highly controversial. Some researchers have stressed the differences

between representations for perception and action [1], others the similarity or even unity of the two [2].

A new study by Antonino Casile and Martin Giese [3], reported in this issue of *Current Biology*, has shown for the first time that motor learning in the absence of vision can directly influence later perceptual performance, a finding that strongly favours the latter perspective. In this study, blindfolded participants were taught to perform novel arm synchronization patterns, patterns that would not normally be observed or executed. Relative to a pre-testing session, all observers showed improved post-learning visual recognition of biological motion displays [4,5] that specifically matched the learned motor patterns. Performance did not improve for visual displays that were

unrelated to the learned motor patterns. Furthermore, a strong correlation was found between how well an individual could perform the motor pattern and the magnitude of the specific recognition advantage.

Such a direct and specific coupling of action and vision is consistent with evidence that action observation often recruits areas of cortex primarily concerned with the control of movement. On a neuronal level, such evidence was first provided through the discovery of so-called 'mirror neurons' [6]. These neurons, located in the parietal and pre-motor cortex of the macaque monkey, fire both when the animal performs an action itself — for example, grasping a nut — and when they observe the experimenter performing the same action. Brain imaging studies have provided ample evidence that a similar mirror system exists in the human brain. This system comprises pre-motor and parietal areas, which are consistently activated when individuals observe actions, engage in motor imagery or perform actions themselves [7]. Importantly, activation of the mirror system is greater when observers are

experts at performing the observed actions [8].

What might be the function of such a direct coupling between perception and action? One obvious function would be the use of perceptual constraints to help learn and refine new movement patterns through overt imitation. When first being shown a new complex movement sequence — for example, a dance routine or martial arts pattern — an observation-execution feedback cycle is clearly a crucial part of learning. The findings reported by Casile and Giese [3] are so striking because they clearly suggest that such a process also works in reverse. That is, the acquisition of new motor skills appears to be able to directly change the way we see the world. Not only vision-for-action, but also action-for-vision. As vision and action typically co-occur in everyday life, this less intuitive outcome may, until now, have been obscured.

Why might it be useful to have action directly affect vision in this way? A main function of the mirror system is thought to be action understanding [6]. In this view, mapping the perceived actions of others' onto one's own action repertoire allows the observer to derive underlying goals. If updating (or even just activating) an action repertoire also affects visual perception, such a link might help accomplish action understanding by, quite literally, allowing us to see the world through someone else's eyes. Another proposal is that the mirror system helps to more directly predict the visual outcome of observed actions [9]. Here it is suggested that the motor system can be used to emulate observed action, helping to project the future course of an event and to stabilize perception in a top-down manner, for example by resolving perceptual ambiguities. Again, updated action repertoires could help improve prediction and anticipation.

While the above proposals may seem reasonable, it would be fair to ask why the visual system

would need help to accomplish either of these goals — action understanding or stable prediction? Put another way, what exactly does the motor system bring to such a marriage? The answer, quite simply, may be time. It is uncontroversial that action representations have both a spatial and temporal component. Our ability to remember and reproduce complex motor patterns clearly relies on such 'dynamic', spatio-temporal representations. Space is the dimension that is typically more emphasised in vision, with the role of time, at least in representation, still being much neglected [10–12]. The suggestion here is that the motor system could be providing vision with a general framework within which to represent and process time, or more specifically, change-over-time [13].

Indeed time may play a crucial role in explaining how learning a new motor skill could lead to more accurate visual perception in Casile and Giese's study [3]. Such a finding is not a straightforward prediction of all theories that assume direct perception-action links, as the authors seem to suggest. Most of these theories assume that an associative link between a movement and its visual outcomes needs to be created before a resonance between perception and action can occur [6,14]. As observers in Casile and Giese's [3] experiment learn a new coordination pattern between familiar movement components, these components would already be linked to a visual consequence. Thus, learning a new temporal coordination pattern on the motor side most likely resulted in improved temporal parsing for the visual elements linked to these motor components.

More generally, a temporal advantage of connecting vision and action clearly has implications that go beyond the perception of the body itself [3,15–17]. Could our overall perception of the dynamic world be mediated by motor experience? Do action

repertoires influence the visual perception of other objects? Might athletes with specialities involving rapid, 'high-frequency' movements, such as martial arts or fencing, come to experience space and time in a different way to those involved in more fluid, 'low-frequency' sports, such as skiing or surfing? The challenge for future research will be not only demonstrate that such effects exist, but also to separate out the influence of motor experience from accompanying visual experience. Casile and Giese [3] have shown that such a separation is possible. The goal now is to apply such methods to other relevant areas of perception [18–20] to more fully assess the role our bodies play as moving windows on the world.

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¹Department of Psychology, University of Wales Swansea, Singleton Park, Swansea SA2 8PP, UK. ²Psychology Department, Rutgers, The State University of New Jersey, Campus at Newark, Smith Hall, 101 Warren Street, Newark, New Jersey 07102, USA. E-mail: I.M.Thornton@Swansea.ac.uk; knoblich@psychology.rutgers.edu

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Morphogens: Precise Outputs from a Variable Gradient

The morphogen gradient as a source of embryonic patterning is one of the best accepted concepts in developmental biology. Morphogens can be transcription factors or extracellular signals, but in both cases they are thought to provide concentration thresholds that position different cell fates within the developing embryo. Several recent papers examine the patterning activities of *Drosophila* Bicoid, the first known molecular morphogen, and reach different conclusions about the patterning power of a single morphogen gradient.

Gozde Yucel and Stephen Small*

The idea that gradients of morphogens are involved in patterning complex embryo body plans has a long history in developmental biology. The morphogen idea was first postulated by Morgan at the beginning of the 20th century, but it was Wolpert [1] who refined the idea in the 1960s. He proposed that different genes would be turned on in response to different threshold concentrations of the morphogen. In Wolpert's French flag model, these states were represented by different colors, with high concentrations turning on a blue gene, lower concentrations turning on a white gene, with red a default state in regions of the embryo below the threshold.

The first morphogen known molecularly was Bicoid (Bcd), a homeodomain-containing transcription factor that is critical for the establishment and placement of all anterior structures in the *Drosophila* body plan. The experimental evidence supporting Bcd as a morphogen is very convincing. Embryos containing different copy numbers of the *bcd* gene show dramatic shifts of landmark structures

along the anterior-posterior (AP) axis [2]. For example, the cephalic furrow, one of the first distinguishable morphological features, is shifted posteriorly in embryos that contain four or six copies of the *bcd* gene.

bcd mRNA is anchored by the cytoskeleton to the anterior tip of the oocyte (Figure 1A) [3]. When eggs are laid, *bcd* mRNA is translated, and a gradient of protein is formed, with highest levels near the anterior tip of the embryo, and progressively lower levels toward posterior regions [4]. The shape of the gradient is thought to be controlled by a combination of the rates of translation, diffusion, and degradation.

While the Bcd protein gradient is forming, zygotic nuclei are undergoing ten very rapid division cycles and migrate to the periphery of the embryo and the early cytoplasmic gradient is converted into a nuclear gradient (Figure 1B). The total amount of Bcd protein in the embryo increases until the beginning of division cycle 14, from when its expression starts to decline [4]. The peripheral migration of the nuclei coincides with the onset of zygotic transcription, and the zygotic

genes *hunchback* (*hb*) and *orthodenticle* (*otd*) are among the first to be turned on by Bcd (Figure 1C). *hb* is expressed throughout the anterior half of the embryo, while *otd* is expressed in only the anterior-most 30% [5, 6]. Initially, these expression patterns are diffuse, but they are refined during nuclear division cycle 14, exhibiting sharp posterior boundaries that are precisely positioned along the AP axis and show very little variation between individual embryos.

If *otd* and *hb* are regulated primarily by Bcd dependent activation, and if the Wolpert model for morphogen activity is

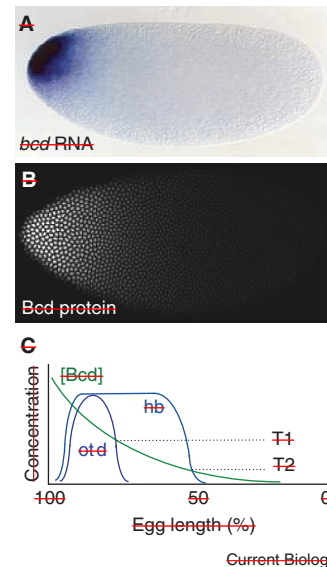


Figure 1. The Bicoid gradient. *bcd* mRNA (A) and protein (B) expression in early *Drosophila* embryos. (C) A schematic model of Bcd morphogenetic activity showing two target genes (*hb* and *otd*) that may respond to different concentration thresholds. (A, C) Reproduced with permission from [18]. (B) Reproduced with permission from the embryo tu9 entry of the FlyEx database (Copyright 1998, David Kosman and John Reinitz).