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Binocular Vision and Stereopsis Across the Animal Kingdom

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Abstract

Most animals have at least some binocular overlap, i.e., a region of space that is viewed by both eyes. This reduces the overall visual field and raises the problem of combining two views of the world, seen from different vantage points, into a coherent whole. However, binocular vision also offers many potential advantages, including increased ability to see around obstacles and increased contrast sensitivity. One particularly interesting use for binocular vision is comparing information from both eyes to derive information about depth. There are many different ways in which this might be done, but in this review, I refer to them all under the general heading of stereopsis. This review examines the different possible uses of binocular vision and stereopsis and compares what is currently known about the neural basis of stereopsis in different taxa. Studying different animals helps us break free of preconceptions stemming from the way that stereopsis operates in human vision and provides new insights into the different possible forms of stereopsis.

INTRODUCTION

Binocular stereopsis: the ability to gain information about the 3D structure of visual scenes by comparing retinal images in two eyes with different lines of sight to the same point in space

Humans have an enormous binocular overlap of some 120° between the fields of view of the two eyes (Spector 1990). Thus, virtually everything that we are aware of seeing is seen twice, once through each eye, yet we perceive our surroundings as if from a single cyclopean point of view (**Figure 1*a***). How this binocular single vision is achieved and "why in seeing with both eyes we do not always see double" (Smith 1738, p. 48) are among the oldest questions in vision research, exercising minds since Aristotle, Ptolemy, and Ibn al-Haytham (Wade & Ono 2012). The value of studying binocular vision as a tool for probing the neural correlate of consciousness was highlighted by Descartes and Sherrington (Sherrington 1906), and it is still actively used in this way today (Crick 1996, Maier et al. 2012).

Binocularly, primates are quite unusual, with frontal eyes and exceptionally wide binocular overlap. Since Wheatstone's (1838) discovery of stereoscopic vision, binocular vision has been linked closely to binocular stereopsis, which was originally believed to be restricted to primates. Virtually all animals have some binocular overlap, however, and the number of animals found to have some form of stereopsis is increasing. Yet our thinking about stereopsis is still highly anthropocentric. Even in papers on nonprimate vision, it is common to find misconceptions such as the idea that stereopsis requires high visual acuity, frontal eyes, or a large binocular overlap (the horse disproves all three); that a large binocular overlap must represent a specialization for stereopsis; or that stereopsis is useful only at short range. Even writers taking an explicitly comparative approach, like Walls (1942), make assumptions clearly driven by human experience: for example, that animals with a binocular overlap must necessarily also achieve binocular fusion and stereopsis.

In this article, I think in theoretical terms about binocular vision and stereopsis, without making assumptions beyond a bilaterally symmetric body plan; for example, I consider the different constraints that apply to simple camera-type eyes versus insect compound eyes. I also consider the pros and cons of a binocular overlap and how these might pay off for different species. In particular, I focus on stereopsis, which I define very generally as the ability to gain information about the 3D structure of visual scenes by comparing retinal images in two eyes with different lines of sight to the same point in space. Once believed to be limited to primates, this ability is now known to have evolved multiple times in different taxa (Nityananda & Read 2017). This observation leads

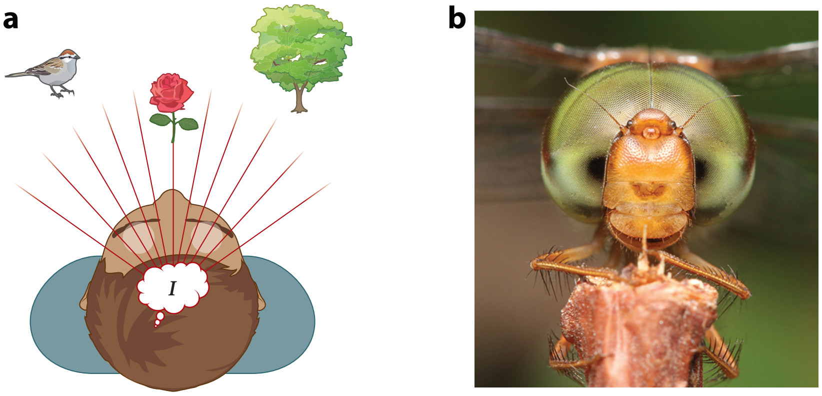

Figure 1

(*a*) Schematic of my perception of how I view the world: as if from a single point somewhere between my eyes. (*b*) Slender duskdarter (*Zyxomma petiolatum*) with compound eyes wrapping around head. Such a species presumably could see the world physically from a single point, formed by the intersection of the optical axes of all of the facets of its compound eye. Image courtesy of Eddy Lee Kam Pang.

to consideration of different forms of stereopsis and what we know about how it works in different species. Stereopsis in other species provides existence proofs for viable forms of stereopsis very different from our own and possible inspiration for new machine stereo algorithms.

WHEN TWO EYES ARE BETTER THAN ONE: REASONS TO HAVE A BINOCULAR OVERLAP

By definition, a binocular overlap means viewing the same region of space twice. This seems wasteful, reducing the total visual field. Yet almost all animals have a binocular overlap, which is in many cases very substantial. Even most compound-eyed animals have separated eyes with overlapping fields of view, even though, in theory, their faceted eyes could view the entire visual sphere from a single projection viewpoint with no overlap (**Figure 1*b***). Since the discovery of stereopsis (Wheatstone 1838), it has often been assumed that stereopsis is the primary advantage of a binocular overlap (Walls 1942). However, as summarized in **Table 1**, there are many other potential advantages.

One simple advantage is redundancy. For many animals, the frontal region is most relevant: It is the space that they enter when they move and where they manipulate objects, whether that manipulation is a praying mantis striking at prey or a starling inspecting the contents of its beak. Having this region covered twice means that loss of or damage to one eye is less disabling. Vertebrate simple eyes have blind spots due to the optic disk (and, additionally, the pecten in birds or conus papillaris in reptiles), and a binocular overlap can compensate for these.

A second advantage is having a monocular view of this critical frontal region—not so much binocular vision as contralateral vision (Martin 2009). This could facilitate judgments such as the angular separation between two objects, which might be more time consuming or less precise if the views from the two eyes had to be stitched together first (B. G. Cumming, personal communication). In birds, Martin (2009) has proposed that contralateral vision may be particularly important for optic flow, where the heading direction is given by the center of expansion (**Figure 2**). It might be easier or quicker for the animal to identify its heading direction if the center of expansion is contained in the monocular view seen by each eye individually. Martin (2009) proposed this for birds, where neural processing remains monocular until later in the visual pathways than in mammals due to an almost complete decussation of the optic nerve. The possibility may also be worth considering in insects such as bees, where early processing is

Table 1 Summary of benefits of a binocular overlap

Benefit of binocular overlap	Eye type to which it applies	Requires binocular information to be combined	Large interocular separation
Redundancy in case of damage	All	No	Irrelevant
Contralateral vision, e.g., for optic flow	All	No	Irrelevant
Improved sensitivity	All	Not necessarily, but functions better with	Irrelevant
Avoidance of frontal blind zone	Simple	No	Unhelpful
Compensation for blind spot at optic disk	Vertebrate simple	Not necessarily	Irrelevant
Frontal optic axes for high resolution	Simple	No	Irrelevant
Seeing around obstacles	All	Not necessarily	Helpful
Stereopsis	All	Yes	Helpful

Stereopsis in this case refers very generally to any distance information obtained from binocular information. This could be used for absolute distance, relative distance, object boundaries and scene segmentation, object shape and recognition, camouflage breaking, motion in depth, optic flow, locomotion, orientation to stimuli, etc.

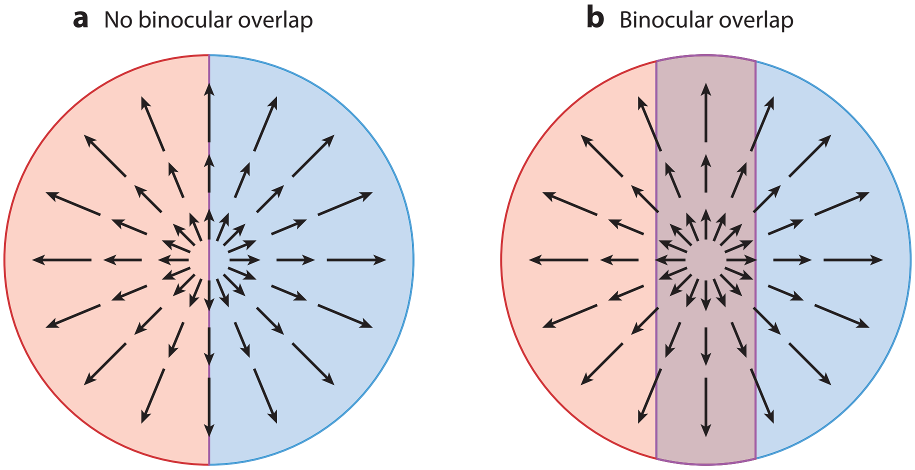

Figure 2

Optic flow fields for an animal heading straight forward. The visual field of the left eye is shaded for an animal with (*a*) no and (*b*) some binocular overlap. We can imagine finding the center of expansion by looking for a point in the neighborhood in which the net flow is zero. In panel *a*, where there is no binocular overlap, no such point exists in either eye; information has to be combined from both eyes to confirm that the heading is straight forward. In panel *b*, the binocular overlap means that the center of expansion can be identified in each eye individually.

also monocular, optic flow is important, and there is a substantial binocular overlap (Kelber & Somanathan 2019, Linander et al. 2015, Taylor et al. 2019).

For species with simple eyes, the centers of the projection of the two eyes are necessarily offset, so a binocular overlap is essential to minimize the blind zone immediately in front of the animal (**Figure 3**). The blind zone extends out to a distance $Z_{\text{blind}} = 0.5I/\tan(0.5\beta)$ from the interocular axis, where I is the distance between the centers of projection, and β is the binocular overlap; increasing β thus reduces Z_{blind}. In birds, species with shorter bills tend to have more binocular overlap (Tyrrell et al. 2017), consistent with selection pressure to reduce the blind zone in front of the body.

A binocular overlap can also provide a form of what has been dubbed X-ray vision, since one eye can see into the blind region created when a nearby object blocks the view in the other eye (Changizi & Shimojo 2008, Otto et al. 2010) (see **Figure 8** below). This ability to see around obstacles may be why "well developed eyes set relatively far apart seem to be an especially common feature among insects living in the densely structured habitats of tropical rainforests" (de la Motte & Burkhardt 1983, p. 459), with the stalk-eyed fly being a particularly extreme example (**Figure 4**).

In the animal in **Figure 3*b***, the binocular overlap is entirely in the peripheral visual field, i.e., far from the optical axis. In humans, we are used to thinking of peripheral vision as being very low resolution because it is far from our fovea. In birds, the fovea is similarly close to the optical axis, looking laterally. However, many birds, including such diverse species as hawks, hummingbirds (Lisney et al. 2015), and pigeons (Bloch & Martinoya 1982), have an additional acute zone in their temporal retina, looking frontally into the binocular field. This ameliorates the neural limits on peripheral vision. However, the optical limits are harder to overcome. For oblique rays, the optical quality of most imaging systems deteriorates away from the optical axis (Artal 2015, Atchison & Thibos 2016). This places optical limits on the resolution of peripheral vision, especially when the pupil is large. If a simple-eyed species needs optimal resolution directly ahead of it, then it

Optical axis: the axis of symmetry of the cornea and lens; along the optical axis, light rays pass undeviated through the eye, and the optical quality of the image is highest

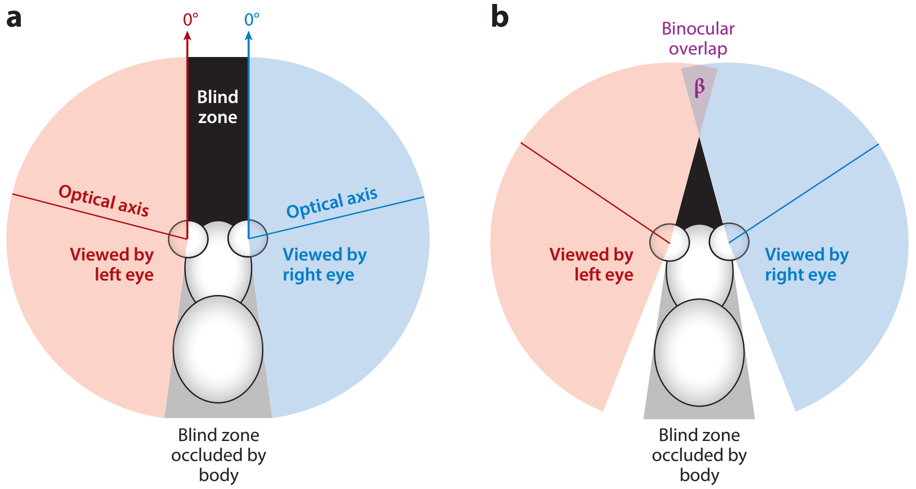

Figure 3

Hypothetical animal with two simple eyes, each with a field of view of nearly 180°. The lines near the center of each visual field represent the optical axes (with the visual field shown extending further temporally than nasally, as in humans). (*a*) A case with no binocular overlap and with a blind zone in front of the animal. The existence of the blind zone is obscured by conventional representations of visual fields, as in **Figure 2**, which represent the fields in terms of angles measured from each eye separately. In that representation, the visual fields of the left and right eyes of this animal meet, since both include the direction 0° (straight ahead, as labeled), making it easy to forget that, in spatial terms, there is a huge blind zone. (*b*) A case with binocular overlap by an angle β, reducing the anterior blind zone at the cost of reducing the field of view. If the interocular separation between the two centers of projection is I, and the binocular overlap is β, then the blind zone in front of the animal extends out to $Z_{\text{blind}} = 0.5I/\tan(0.5\beta) \sim I/\beta$. Thus, increasing the binocular overlap reduces the blind zone.

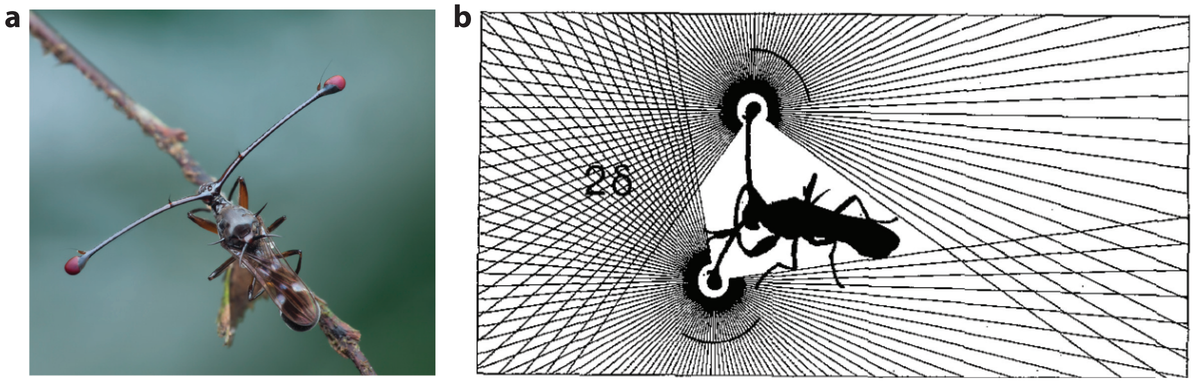

Figure 4

(*a*) The Asian stalk-eyed fly, *Cyrtodiopsis whitei*, (*b*) has high spatial resolution (interommatidial separation of 1.3° in the acute zone) and a huge anterior binocular overlap of 135°, as well as a narrow overlap behind (de la Motte & Burkhardt 1983). Its behavior (jumping on prey, distant-dependent orientation, grasping prey, taking off into flight both forward and backward) suggests that it may use its binocular zones for stereopsis, as well as for seeing around obstacles. Panel *a* image courtesy of Melvin Yeo. Panel *b* reproduced with permission from de la Motte & Burkhardt (1983).

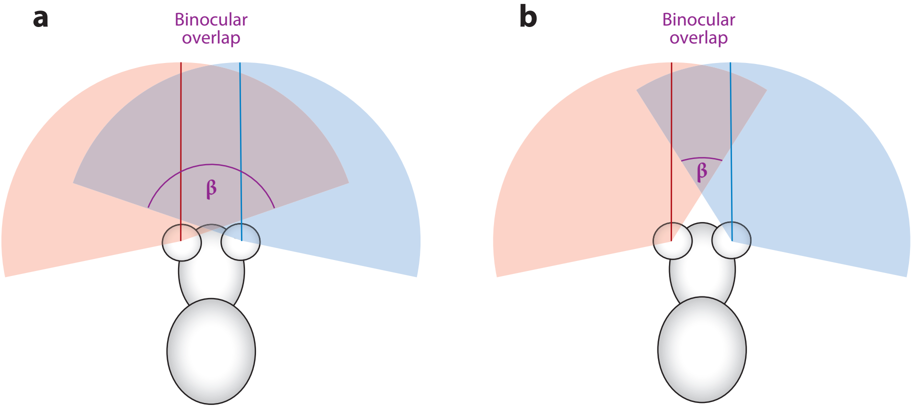

Figure 5

Frontal eyes do not mandate a wide binocular overlap. Hypothetical animals with frontal eyes and parallel optical axes are shown. (*a*) Situation approximating that of humans viewing infinity, with very wide binocular overlap. (*b*) Optical axes remain parallel, but the nasal visual field is trimmed to limit the binocular overlap. This increases the monocular region along each optical axis, which extends a distance $Z_{\mathrm{monoc}} = I/\tan(\beta/2)$. For humans, truncating the nasal field at 20° eccentricity would save tissue without affecting our total visual field or our stereopsis. While a human is looking into the distance, this would extend the frontal blind zone to approximately 9 cm and mean that the first approximately 20 cm in front of each eye was viewed monocularly.

needs to bring its optical axes forward so as to direct them parasagittally (for distant objects, as in **Figure 5**) or even across the midline (to converge on near objects). This has been adduced as a reason for the front-facing eyes of nocturnal predators such as cats and owls, where pupils need to be large to capture the available light, and thus, optical aberrations degrade the image more severely than in other species (Allman 1977, Cartmill 1997, 2018).

It has been postulated that primates have frontal eyes because their ancestors were nocturnal predators. However, simian primates also have particularly high visual acuity; they are the only mammals with a foveal pit, a neural adaptation for high acuity that would be wasted by poor optics. Even diurnal primates, therefore, may have needed front-facing optical axes to match their front-facing fovea. If so, this process seems not to have evolved to completion: In humans, the fovea is significantly offset from the optic axis by some 5° temporally and 2° downward on the retina (Bennett & Rabbetts 1989). This means that, when we look straight ahead into the distance with parallel visual axes, our optical axes diverge slightly for reasons that are unclear.

The wide binocular overlap of primates is often cited as an adaptation for stereopsis. However, this seems unlikely. True, frontal optical axes enable high acuity in the space in front of the animal, which in turn improves stereoacuity—although this benefit is partially offset by the reduced depth resolution associated with the lower interocular separation (Cartmill 1997). However, the wide binocular overlap, which extends to eccentricities of 60°, is not exploited for stereopsis in humans: Stereopsis decays rapidly with eccentricity and has not been demonstrated beyond approximately 15° (Blakemore 1970, Ghahghaei et al. 2019, Parker 2007, Richards & Regan 1973, Siderov & Harwerth 1995). If a wide binocular field were not required, then it would have been possible to keep the optical axes frontal but save neural tissue and processing costs by trimming the nasal visual field beyond 15°, as in ***Figure 5b***. This trimming has evolved in the short-toed eagle, where there is no retina serving the nasal margin of the optical field (the region of space imaged through the pupil) (Martin & Katzir 1999). In humans, the far nasal periphery is retained but

Visual axis: line of sight to highest-acuity point in the retina; in humans, offset by a few degrees from the optical axis

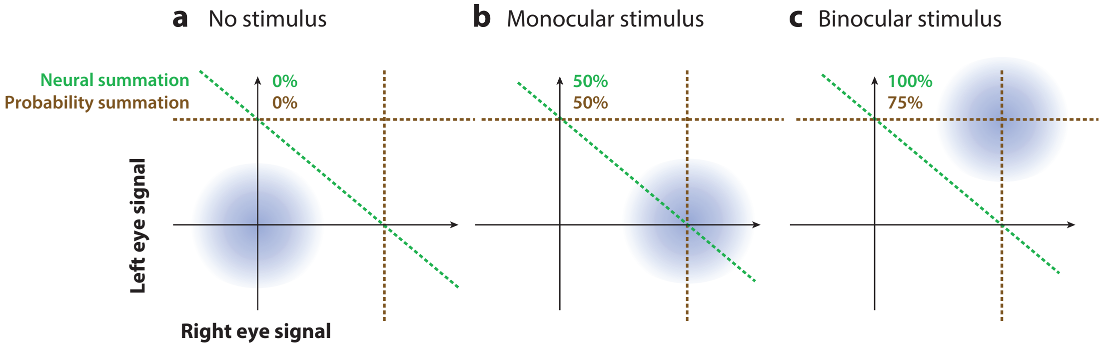

Figure 6

Binocular summation when detecting a stimulus. Each eye contributes a noisy signal. Probability summation occurs when the stimulus is detected if the signal in either eye exceeds a threshold indicated by the brown dashed lines parallel to the axes. With the noise and thresholds indicated, the animal thus (*a*) correctly never perceives a stimulus when none is present, (*b*) perceives the monocular stimulus 50% of the time, and (*c*) perceives the binocular stimulus 75% of the time. Neural summation would occur if, instead, signals from each eye were averaged before being compared to a threshold. The detection boundary would then be diagonal (*green dashed line*). This particular boundary was chosen such that the detection probability is still 50% for the monocular stimulus in panel *b*, but the binocular stimulus in panel *c* is detected 100% of the time. Neural summation therefore offers a greater binocular advantage than does probability summation. In humans, the binocular combination is nonlinear (Baker et al. 2018, Legge 1984).

stripped down. Where stereopsis ceases to operate, there is a pronounced nasal–temporal asymmetry, with the nasal visual field beyond 20° eccentricity having a lower retinal cell density, less cortical representation, and lower sensitivity (Anderson et al. 1991, Curcio et al. 1990, Fahle & Schmid 1988).

One reason for retaining the nasal field may be to minimize the frontal blind zone. A second may be to maintain the ability to see around obstacles across a wide area of the visual field. A third reason, especially for nocturnal animals, may be to enhance sensitivity. Two eyes are better than one in that they give two chances to detect something via probability summation (Blake & Fox 1973). If the probability of detecting a stimulus in one eye is P_{monoc}, then the probability of detecting it with two independent eyes is greater by a factor[1] of $P_{\mathrm{binoc}}/P_{\mathrm{monoc}} = (2 - P_{\mathrm{monoc}})$ (see **Figure 6**, where $P_{\mathrm{monoc}} = 50\%$ and $P_{\mathrm{binoc}} = 75\%$). This advantage is greater with lower P_{monoc} and is thus especially valuable in environments where visual stimuli are hard to detect, e.g., at night. Humans generally show an even greater binocular advantage, which is thought to occur because the two eyes' inputs are combined before being thresholded (**Figure 6**). This neural summation allows independent noise from the two eyes to average out, offering a greater binocular advantage (Baker et al. 2018, Blake & Fox 1973, Blake et al. 1981, Legge 1984, Movshon et al. 1978, Rose et al. 1988, Tyler & Chen 2000).

Comparative studies have found an association between wide binocular overlap and nocturnality in many taxa (Heesy 2008, Ravosa & Savakova 2004, Smith et al. 2018, Vega-Zuniga et al. 2013). Nocturnal bees such as the Indian carpenter bee have several adaptations for low-light conditions (Somanathan et al. 2009), which may include some form of binocular summation, as well as neural summation within an eye (Kelber & Somanathan 2019, Somanathan et al. 2009, Warrant 2008). A nocturnal parrot, the kākāpō (**Figure 7**), has evolved front-facing eyes and a wide binocular overlap (Corfield et al. 2011). Freely moving rats have disconjugate eye movements that

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[1] The stimulus is missed binocularly only if it is missed in both eyes: $1 - P_{\mathrm{binoc}} = (1 - P_{\mathrm{monoc}})^2$. This reduces to give the ratio in the text.

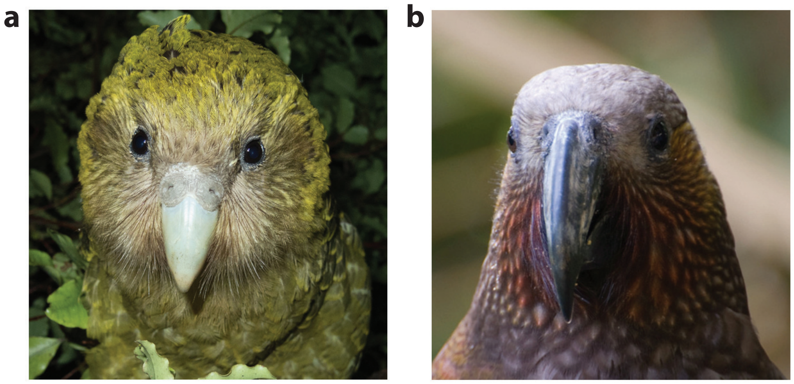

Figure 7

(*a*) The kākāpō or night parrot, *Strigops habroptilus*, also called the owl parrot for its frontal eyes and facial ruff. (*b*) For comparison, its close relative, the diurnal kākā, *Nestor meridionalis*, which has lateral eyes. Images courtesy of Dr Andrew Digby, New Zealand Department of Conservation.

nevertheless maintain a binocular field overhead, where the dark shadow of a potential predator will send the rat scuttling for shelter (Wallace et al. 2013). In humans, binocular summation extends into and even strengthens in the far periphery, at least for large objects and low spatial frequencies (Wakayama et al. 2005, 2011; Wood et al. 1992; Zlatkova et al. 2001). It may also improve resolution by combining the sparse peripheral sampling in each eye (Zlatkova et al. 2001). All of this is consistent with the idea that a wide binocular overlap may often have evolved to provide a wide region of binocularly enhanced sensitivity, with—in humans at least—stereopsis being restricted to a much smaller central subregion of the binocular field.

INTEROCULAR SEPARATION

In studies of comparative morphology, like those cited above, much more attention has been paid to the width of binocular overlap than to the interocular separation. Yet the latter is more fundamental in unraveling the possible function of a binocular overlap. Consider the two extremes shown in **Figure 8**, with identical monocular visual fields and binocular overlap (expressed as an angle; see **Figure 3**). In **Figure 8*a***, the eyes are close enough together and have low enough resolution, and relevant objects are distant enough, that the lines of sight from each eye are effectively parallel. Such a species could not use its binocular vision for stereopsis or for seeing around obstacles, but it could still benefit from improved sensitivity and resolution. Conversely, in **Figure 8*b***, resolution and eye separation are high enough, and distances short enough, that angles between lines of sight are often appreciable, giving an animal the ability to judge depth and see around obstacles. The kākāpō (**Figure 7**) and stalk-eyed fly (**Figure 4**) may approximate these extremes.

To quantify this, we define the angle subtended by the interocular separation at an object as the object's headcentric disparity, $\Delta\theta$ (**Figure 9**). For distant objects, this is approximately $\Delta\theta \approx I/Z$, where I is the interocular separation, and Z is the perpendicular distance of the object from the observer. The minimum detectable change in disparity can be written as ε, and stereopsis works up to $Z_{\max} \sim I/\tan(\varepsilon)$ (distances beyond $Z_{\max}$ cannot be distinguished from infinity), while the minimum detectable change in distance, starting from Z, is $\delta Z \sim Z^2 \tan(\varepsilon)/I$. Thus, for a given ocular resolution, increasing interocular separation both extends the range of stereopsis and makes it more precise.

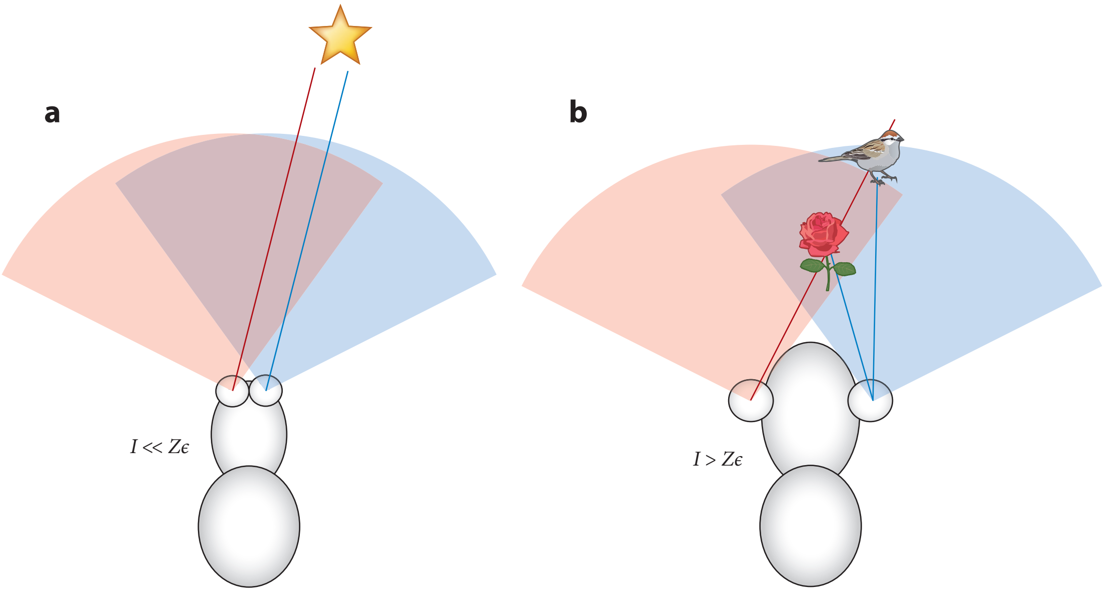

Figure 8

Two qualitatively different forms of binocular vision. (*a*) The headcentric disparity i.e., the angle subtended by the interocular separation I at ecologically relevant distances Z, is negligible compared to the visual resolution ε in radians. Objects effectively have the same head-centric direction in both eyes, so binocular fusion is simplified (although, if the eyes can converge, then it may not be entirely trivial). Sensitivity and acuity benefits can be obtained essentially by averaging the two images. However, seeing around occluders and stereopsis are not possible. (*b*) The headcentric disparity is significant. This means that, even if the eyes are fixed in the head, the direction to the object may differ in the two eyes, with a difference (disparity) depending on its distance. This makes binocular fusion potentially complex. However, it enables stereopsis (for example, deducing that the flower is closer than the bird from their different disparities) and seeing around obstacles (the bird is visible to the right eye even though the flower hides it from the left eye).

In humans, the conservative estimates $\varepsilon \sim 20$ arcsec and $I \sim 6$ cm give a theoretical range for stereopsis of $>$600 m, which has been confirmed up to 250 m (Palmisano et al. 2010). Thus, while human stereopsis may be most useful within arms-length or next-step distances, it is available at distances far beyond them. In horses, where $\varepsilon \sim 15$ arcmin and $I \sim 20$ cm, the predicted range is 45 m (Timney & Keil 1999). In the stalk-eyed fly (**Figure 4**), the interommatidial separation of ~1° and $I \sim 10$ mm suggest a possible range of 60 cm; in the African lined mantis, the acute-zone interommatidial angle of ~0.5° and $I \sim 7$ mm suggest a range of approximately 80 cm. In an admittedly speculative study, Stevens (2006) estimated that stereopsis might have extended out to 6 km in *Tyrannosaurus rex* (**Figure 10**).

CORRESPONDENCE AND FUSION

The most obvious disadvantage of a large interocular separation is the one with which I begin this review: fusing such different viewpoints into a single view of the world. In general, this requires a judgment about which points in the two eyes correspond to the same object in space and should therefore be fused. This process is referred to as stereo correspondence. Correspondence seems essential not only for stereopsis but also for orienting correctly to objects. For example, the flower in **Figure 8*b*** is in the right visual field for the left eye and the left visual field for the right eye. Only if these two directions are combined can the flower be perceived, correctly, as directly ahead. Walls (1942) argued that any animal with a binocular overlap must achieve correspondence,

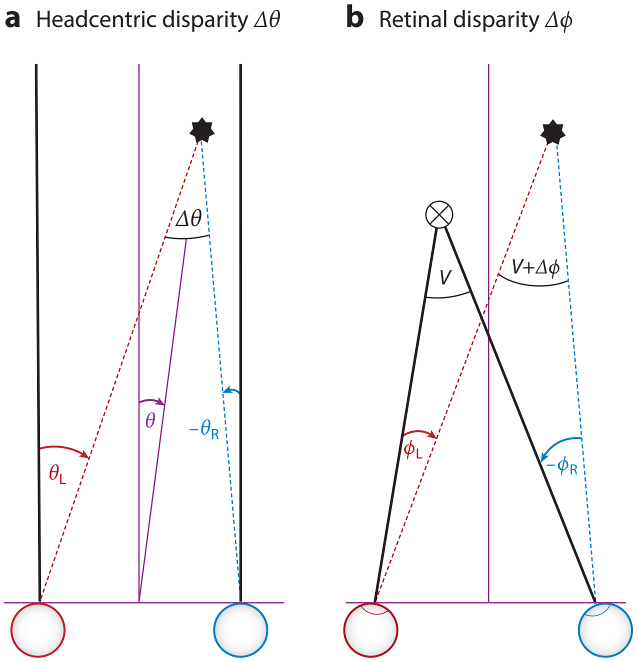

Figure 9

Top-down view of eyes viewing an object. (*a*) Headcentric disparity. Angles θ are defined relative to a parasagittal direction such that objects to the right of each eye have positive angles; thus, θ_R is negative in this example. The object's headcentric disparity is $\Delta\theta = \theta_L - \theta_R$, while its direction relative to the midline is approximately $\theta \sim (\theta_L + \theta_R)/2$. (*b*) Retinal disparity. Angles ϕ are defined relative to a retinal location, e.g., the fovea. The star indicates the fixation point.

Figure 10

Skull morphology suggests that *Tyrannosaurus rex* could have exploited stereoscopic vision. The huge interocular separation of 40 cm, combined with high visual acuity allowed by the 14-cm-diameter orbits, might have allowed unsurpassed stereoacuity. Figure adapted from ScottRobertAnselmo/ (**https://commons.wikimedia.org/wiki/File:Sue_TRex_Skull_Full_Frontal.JPG**) (CC BY-SA 3.0), after Stevens (2006, figure 12B).

binocular fusion, and thus stereopsis, since "they would gain absolutely nothing from binocularity if they saw the object diplopically" (p. 327), and "if they have fusion, they have parallactic localization of the object in space" (p. 328). Yet all of the steps in this logic are open to challenge. A rat simply needs to run for shelter if a dark object appears in its overhead binocular field (Wallace et al. 2013), without needing to perceive the object in a particular direction, let alone estimate its distance; thus, it could benefit from enhanced sensitivity without needing fusion or stereopsis. Humans are capable of gleaning stereoscopic depth information from stimuli whose disparity is too large to fuse and that thus appear double (Mitchell 1969, Ogle 1953), indicating that stereoscopic depth does not necessarily require fusion. Other stereoscopic information is available without any correspondence, for example, interocular velocity difference (Cumming & Parker 1994). As an animal approaches a surface, the surface moves rightward in the nasal hemifield of the left eye and leftward in the nasal hemifield of the right eye. This cue does not require details on the surface to be matched.

Some form of correspondence and fusion is, however, required to get the full benefit of binocular vision. For example, although probability summation can produce a binocular enhancement in contrast sensitivity without fusion, the greater benefit observed with neural summation in humans (**Figure 6**) is only achieved by combining retinal inputs corresponding to the same object (Blake et al. 1981). For this reason, neural summation only occurs for stimuli presented at the same time and in corresponding regions of the retinae.

Animals, such as some insects, with fixed, close-set eyes and low resolution (**Figure 8*a***) could assume correspondence and achieve fusion simply by averaging retinal inputs corresponding to the same line of sight. They would benefit from increased contrast sensitivity and the other advantages for which interocular separation is irrelevant (see **Table 1**). However, for an animal that can use stereopsis or see around obstacles, by definition, objects project to different locations in the two eyes. Both the distance to the object and the current position of the eyes affect which point in the right retina corresponds to the object seen by a given point in the left retina.

In animals with fixed eyes, the correspondence problem is at least one-dimensional. Given a point in the left eye, the set of possible corresponding points in the right eye forms a line, the epipolar line, which is fixed on the retina. In animals with mobile eyes, the epipolar lines depend on eye position and thus move on the retina, making the problem more complex. One way in which mobile-eyed animals address this challenge is by having highly constrained eye movements.

Two mobile eyes could have, in principle, six degrees of freedom: the azimuth and elevation of each visual axis, plus torsion around that axis. However, in species as diverse as humans and chameleons, the oculomotor system removes two degrees of freedom: The same torsions are adopted for given azimuths and elevations. Many mobile-eyed species can switch between two modes of oculomotor control: an independent mode with the full four remaining degrees of freedom, where the eyes move independently to track objects of interest or stabilize their own retinal image, and a binocular mode with just three degrees of freedom, where both eyes fixate on the same object (Brysch et al. 2019, Budelmann & Young 1993, Dearworth et al. 2013, Fritsches & Marshall 2002, Katz et al. 2015, Martin 2009, Ott 2001, Pettigrew et al. 1999, Voss & Bischof 2009, Wallace et al. 2013).

It seems plausible that, in the independent mode, fusion does not occur. Even if a binocular overlap remains, and an object happens to be visible to both eyes, its perceived direction could depend only on its image in one of the eyes, with the other eye's image effectively suppressed or at least not attended, as in humans with alternating strabismus (Butler et al. 2018, Pettigrew et al. 1999, Voss & Bischof 2009). In the binocular mode, when both eyes fixate the same object, one possible solution would theoretically be to fuse the retinal images only at the fixation point. This could enhance contrast sensitivity beyond simple probability summation, while vergence information from oculomotor information could theoretically be used to estimate the distance to the fixated object. Indeed, humans fuse only over a relatively narrow range around fixation, and it is not uncommon to notice physiological diplopia (Ogle et al. 1949, Panum 1858). However, true fusion away from the fixation point requires a solution of the stereo correspondence problem.

Local correspondence: the process of matching up left and right eye images based on the similarity of small image patches

Global correspondence: the process of selecting between competing local matches based on global geometric constraints, such as the requirement that all matches be consistent with a single eye position

LOCAL VERSUS GLOBAL CORRESPONDENCE

The correspondence problem is computationally challenging (Colodro-Conde et al. 2014, Hartley & Zisserman 2000, Liu & Aggarwal 2005, Scharstein & Szeliski 2002). In both the computational and psychological literature, a distinction is made between local and global stereopsis or stereo correspondence. In the computational literature, the distinction is clear: In local stereopsis, correspondence is decided solely by looking for matches between small neighborhoods in each eye, while in global stereopsis, a disparity map is sought simultaneously across the entire image, optimizing local correspondence subject to global constraints or cost functions such as uniqueness (a preference for matching each point in the left eye with exactly one point in the right eye; **Figure 11**), depth smoothness or continuity (a preference for gradual variation in depth), and epipolar geometry (all matches should be consistent with a single eye position) (Liu & Aggarwal 2005, Marr & Poggio 1976). In practice, many algorithms use semiglobal optimization approaches that combine aspects of both (Hirschmüller 2008). In the psychological literature, the usage is much less clear, with papers a few years apart using radically different definitions of local and global stereopsis (Julesz 1978, Richards & Kaye 1974). The most common usage is, I believe, not helpful for reasons discussed below. In this review, the terms local and global stereo correspondence therefore have their computational meanings.

An example of global correspondence in this sense is offered by **Figure 11**. When a single object is presented at $\theta_{L1} = +2\alpha$ in the left eye and $\theta_{R1} = -2\alpha$ in the right (**Figure 11*a***), humans

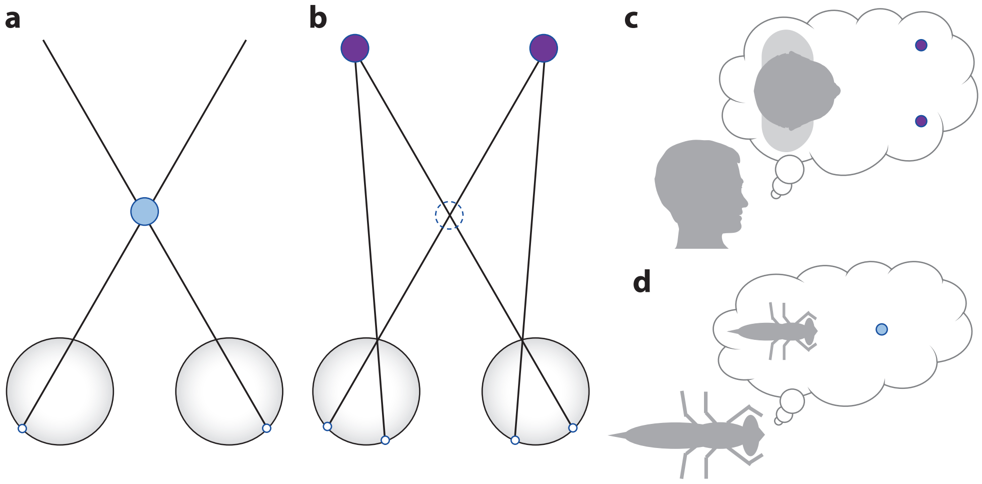

Figure 11

Top-down view of eyes viewing (*a*) one and (*b*) two objects (not drawn to scale). In panel *a*, humans perceive a single object on the midline. In panel *b*, the retinal stimuli are the same as in panel *a* except that an identical retinal image is added medially in each eye. In humans, this abolishes the percept of the object on the midline; (*c*) the percept is now of two more distant, smaller objects on either side of the midline. In contrast, (*d*) the dragonfly larva *Aeshna cyanea* appears to perceive a nearby object on the midline in both cases. I refer to the empty dashed circle in panel *b* as a ghost match: Locally, the two retinal images match perfectly; only global information across the scene indicates that these do not correspond to a real object.

perceive a single object on the midline, as expected from local correspondence, because the retinal image at θ_{L1} perfectly matches that at θ_{R1}. However, when identical retinal images are added at $\theta_{L2} = -\alpha$ and $\theta_{R2} = +\alpha$, humans no longer perceive an object on the midline; instead, they perceive two objects at the same distance on either side of the midline (**Figure 11*b***). The perception of the retinal stimuli at θ_{L1}, θ_{R1} has changed even though nothing has altered locally, reflecting global constraints such as uniqueness and smoothness. Neurally, this could be explained with long-range excitation and inhibition between potential matches at different points in the visual field, with matches at one disparity encouraging potential matches with similar disparity and inhibiting others (Marr & Poggio 1976). These long-range interactions are examples of global, or at least nonlocal, stereopsis. In other respects, however, human stereopsis does a poor job of enforcing global constraints. For example, depth percepts can be inconsistent with any single eye position (Cagenello & Rogers 1993, Kaneko & Howard 1997, Serrano-Pedraza et al. 2010), whereas a decent computational stereo algorithm would make sure to enforce consistent epipolar constraints across the entire visual field (Liu & Aggarwal 2005).

Ghost match: where the left and right image-patches match perfectly, and only a consideration of the global geometry can reveal that they are not views of the same object

Cyclopean stereopsis: a form of stereopsis that can reveal structures such as depth boundaries in the absence of any monocular cue such as a luminance change

Other species may have even less global correspondence than humans. The larvae of the dragonfly *Aeshna cyanea* appear to hunt using stereopsis, but they strike both when a prey item is within the range of their labium (**Figure 11*a***) and when a ghost match is created by two more distant, identical objects (**Figure 11*b***) (Schwind 1989). This result indicates that dragonfly larvae do not achieve global stereopsis.

LOCAL CORRESPONDENCE AND CYCLOPEAN STEREOPSIS

By definition, local correspondence algorithms need some kind of match-quality metric to assess how closely the image patch around a given point in the left image matches patches in the right image. The patches that match most closely are assumed to be viewing the same point in the visual scene. A common metric is some form of normalized interocular correlation (Ackermann & Goesele 2015). A correlation coefficient approaching 1 between pixel values in left and right image patches indicates that the patches agree closely. Human stereopsis is highly sensitive to interocular correlation. Performance falls for any manipulation that reduces correlation, and if stimuli are made anticorrelated by inverting one eye's image, then depth perception is effectively abolished (Hibbard et al. 2014, Julesz & Tyler 1976). This suggests that the matching metric used for human local correspondence is closely related to interocular correlation.

The great advantage of interocular correlation and similar match-quality metrics is that they do not require particular features or objects to have been identified in either eye individually. In fact, this form of stereopsis can detect objects that are invisible monocularly, revealing them via their depth boundaries even if they perfectly match the texture of their background. This ability to break camouflage has been proposed as a reason that primate stereopsis evolved (Julesz 1971). It is of course particularly useful in detecting stationary objects, since motion usually breaks camouflage in itself.

This form of stereopsis is called cyclopean stereopsis, referring to its ability to reveal structures that are not present in the monocular images but can only be seen by a central, cyclopean eye (Julesz 1971, Tyler 1991). The term fine stereopsis is also used, referring to its great precision in humans. It is also referred to as global stereopsis in the psychology literature, reflecting an earlier belief that cyclopean stereopsis required global mechanisms to disambiguate the multiplicity of matches between similar image features. However, our current understanding of human vision emphasizes the role of purely local correlation in cyclopean stereopsis, and there is also evidence for global interactions in noncyclopean stimuli (see **Figure 11**). Thus, although I have done so myself in the past, I believe it is unhelpful to use the term global stereopsis in this sense.

Cyclopean stereopsis has been demonstrated in several nonhuman vertebrates: monkeys (Bough 1970), cats (Ptito et al. 1991), horses (Timney & Keil 1999), mice (Scholl et al. 2013), barn owls (van der Willigen 2000, 2011; van der Willigen et al. 1998), falcons (Fox et al. 1977), and pigeons (McFadden & Wild 1986). The thorough investigations in barn owls have demonstrated a degree of similarity with human stereopsis that is particularly striking given that binocular vision is believed to have evolved independently in mammals and birds (Pettigrew 1986).

INTERPRETING DISPARITY WITH MOBILE EYES

As discussed above, mobile eyes make it harder to extract disparity. They also make it harder to interpret. As **Figure 9*a*** shows, headcentric disparity maps onto a given distance from the animal. Animals with fixed eyes can use this directly to judge absolute distance, whether to the prey that they want to catch or to a branch that they plan to jump onto. However, with mobile eyes, headcentric disparity requires a knowledge of eye position. Without that, all one has is retinal disparity (**Figure 9*b***). I use the symbol ϕ to describe an object's retinocentric location relative to the visual axis, distinct from θ, which describes the object's headcentric location relative to the parasagittal plane through that eye. The absolute retinal disparity of a point is $\Delta\phi = \phi_L - \phi_R$, which is shifted relative to the headcentric disparity by the angle between the visual axes, the vergence angle V: $\Delta\theta = \Delta\phi + V$. In primates, cyclopean stereopsis works for only a small range of retinal disparity, up to two or three degrees (Erkelens 1988, Glennerster 1998).

Humans are very poor at making metric distance judgments based solely on absolute disparity, presumably because of uncertainty in vergence (Erkelens & Collewijn 1985, Johnston 1991, Linton 2020). This is ironic given that vergence was the first binocular depth cue to be identified and was long assumed to be the most powerful cue to distance (Linton 2020, Wade & Ono 2012). It is also surprising, given that information about vergence is potentially available from many sources: from oculomotor signals, e.g., efference copy; from proprioception; indirectly via accommodation; and even from the retinal pattern of disparity itself (Backus et al. 1999, Read et al. 2009, Rogers & Bradshaw 1993). Owls, too, seem to be poor at using absolute retinal disparity, even though they have much more limited eye movements and thus might have been expected to map disparity directly to distance (van der Willigen 2011).

Owls and humans are much better at using relative retinal disparity, i.e., the difference between the absolute retinal disparities of two locations,

$$\Delta\phi_2 - \Delta\phi_1 \approx I/Z_2 - I/Z_1,$$

or, more generally, the gradient of absolute disparity across the retina. This depends only on the distances to the objects, not on eye position (although eye position is still required to convert relative disparity into the distance between the objects). The sign of relative disparity specifies which object is closer, while discontinuities in relative disparity indicate an abrupt change in depth and thus a surface boundary.

Overall, then, cyclopean stereopsis seems to be used to detect surface structure—edges, slant, or curvature—in a relatively narrow window around the fixation point. This may explain why it is found in animals like horses, which do not catch prey or jump onto branches: It may help in rapid locomotion over uneven ground (Bonnen et al. 2019). It may also improve heading judgments using optic flow by providing information about depth order (van den Berg & Brenner 1994).

VERGENCE AND CONTOUR STEREOPSIS

An additional question is how the eyes manage to fixate correctly to begin with. Theoretically, fixation could be achieved monocularly if each eye independently moves to fixate the most salient object. This may indeed be how some species shift from independent monocular to joint binocular oculomotor control, but in humans, oculomotor control is always binocular, so we need other ways of achieving vergence.

One such method is the accommodation of the ocular lens needed to bring an object into sharp focus. This can be demonstrated if, with one eye occluded, the other changes from looking into the distance to focusing on a nearby object of interest; the change in focus causes a convergence movement of the occluded eye. However, humans also seem to benefit from a separate, coarse stereo system that is mainly designed for initiating vergence beyond the range of the fine, cyclopean stereo system (Julesz 1971; Tyler 1991, p. 199). This system seems to be non-cyclopean, i.e., it seems to require monocularly visible features, so I refer to it as contour stereopsis (Fricke & Siderov 1997). It is also less precise and—of course—works over a larger range of disparities than cyclopean stereopsis. There is intriguing evidence that it may work in headcentric coordinates, i.e., that the monocular contours are corrected for eye position before disparity is extracted (Zhang et al. 2010).

Contour stereopsis: a form of stereopsis that can detect disparity between monocularly visible image features but cannot reveal any structure not visible monocularly

Cyclopean stereopsis seems to be more vulnerable than contour stereopsis to disruption by binocular vision disorders. Thus, for people with normal vision, performance is similar on contour versus cyclopean stereotests, since in both cases perception is driven by fine cyclopean stereopsis. In contrast, people with binocular vision disorders may only make use of contour stereopsis and thus may perform worse on cyclopean stereotests (Fawcett 2005, Frisby et al. 1975, Giaschi et al. 2013, Vancleef et al. 2017, Zhao & Wu 2019).

STEREOPSIS WITHOUT CORRELATION

As a tool for local correspondence, binocular cross-correlation seems so computationally simple yet effective that it should be universal. However, two very different invertebrate predators, the praying mantis and the cuttlefish, are insensitive to it (Feord et al. 2020, Nityananda et al. 2018). In both, stimuli depicted in random-dot stereograms evoked the same disparity-dependent attack response, whether the random dots were binocularly correlated or not.[2] Both of these species will only attack moving prey, so the random-dot stimuli had to move across a random-dot background. The correlated stimuli thus contained two forms of disparity: static disparity, defined by the dot pattern in individual frames, and kinetic disparity, defined by the monocular boundaries of the moving patches (Lee 1970). In the decorrelated stimuli, the static disparity cue was disrupted, while the kinetic disparity cue was unaffected. Humans depend almost totally on the static disparity cue, extracted by our cyclopean stereopsis from individual image pairs, and were thus hugely disrupted when the stimuli were decorrelated (Nityananda et al. 2018). The lack of disruption in mantids and cuttlefish suggests that these species depend instead on the kinetic disparity cue.

In mantids, the kinetic disparity cue can be defined by almost any kind of temporal change. Mantids do not require translation of particular image features around a scene (first-order motion); they can also detect disparity in second-order motion stimuli, for example, a random pattern of black and white dots where the dots do not move, but instead change from white to black or vice versa as the notional target passes over them (Nityananda et al. 2019). This suggests a form of contour stereopsis that do not operate directly on the pattern of contrast in left and right eyes, but instead operates on some measure of how that pattern is changing over time. This could be as simple as a high-pass temporal filter followed by rectification (Nityananda et al. 2019). Thus,

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[2] Mantids were tested with random-dot stimuli that were binocularly correlated, anticorrelated, or uncorrelated. In the first-order motion stimulus, cuttlefish were tested only with correlated and anticorrelated stimuli (T.J. Wardill, personal communication).

Strong correspondence: a neuron implementing strong correspondence is sensitive to the similarity between single pairs of images, in addition to its sensitivity to monocular images

Weak correspondence: a neuron implements weak correspondence if it does not show strong correspondence but still responds more strongly on average to matching than to mismatched images

although the moving-target random-dot patterns input to each eye are cyclopean as far as human stereopsis is concerned, in that the moving target is invisible in any one monocular image, after temporal filtering, the stimulus has clear monocular contours at the leading and trailing edges of the moving target.

Cuttlefish did not attack targets defined by second-order motion at all, although they did engage with them: They swam toward the stimuli and followed them but did not strike. This was again true regardless of the binocular contrast correlation.[3] This result does not support the idea of a front-end to cuttlefish stereopsis in which an image is highpass filtered and then rectified, but it also does not rule this out. A key difference may be that the cuttlefish made some effort to track the moving targets, both with their bodies and with their mobile eyes, whereas mantids have fixed eyes, were fixed in place, and made only small head movements. Tracking could greatly alter the spatiotemporal contrast between target and background in the two conditions. With perfect tracking, in the first-order case, the dots defining the target would be static on the retina and thus retain high contrast, and the background dots would stream backward, while in the second-order case, all dots would stream backward and thus effectively have low contrast. This lower effective contrast could make it harder for animals to discriminate the detailed shape of the target, and since cuttlefish strike only at stimuli that resemble a shrimp in some detail (T.J. Wardill, personal communication), this could lower the strike rate. This illustrates a general asymmetry in experiments that exploit an animal's natural behavior: A positive response proves that the system can detect the stimulus, but a negative response does not prove that it cannot.

Toads, similarly, have only been tested with monocularly visible moving targets (Collett 1977). There is thus currently no evidence for cyclopean stereopsis outside mammals and birds; only contour stereopsis has been demonstrated in amphibians, cephalopods, and insects.

NEURAL COMPUTATIONS FOR LOCAL CORRESPONDENCE

Whether the stimuli are cyclopean or contour, local correspondence requires a comparison between small patches of the left and right images, with sensitivity to the degree to which these patches match. The meaning of local will vary between species, but a good working definition is comparable to the size of behaviorally relevant visual features, such as prey. To be more precise about correspondence, it is useful to define weak versus strong correspondence. Consider two different image patches, a and b. Suppose that these both drive a particular neuron equally well, i.e., the neuron's firing rate is the same whether both eyes see a or both eyes see b. For strong correspondence, this matched-image response should be greater than the mismatched response when one eye sees a and the other sees b. However, as we see below, a neuron might fail this test and yet still, on average over all images, fire more when the two image patches are the same than when they are different. I refer to such a neuron as implementing weak correspondence.

Consider a hypothetical linear binocular neuron that receives inputs L, R from earlier monocular neurons and sums them: $B = (L + R)$. For simplicity, I assume that the monocular processing is identical,[4] so that a given image patch a gives the same monocular input in either eye: $L(a) = R(a)$ for all a. Clearly, this neuron does not implement strong correspondence, since if two image patches give the same monocular responses, $L(a) = L(b)$, then $B(a,b) = B(a,a) = B(b,b)$. In fact,

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[3] Uncorrelated dots were only tested with second-order motion. The apparent difference between anticorrelated and uncorrelated stimuli in Feord et al (2020), therefore, most likely reflects a difference between first-order and second-order motion (T.J. Wardill, personal communication).

[4] This is equivalent to assuming zero phase disparity. This assumption streamlines the argument, but the conclusions can be generalized.

this linear computation cannot implement even weak correspondence. To see this, note that for matching images, $R = L$, so the average value of the sum $(L + R)$ across all matching image pairs is $2<L>$, where $<L>$ represents the average value of L across all (possible, or ecologically relevant) images. The average value of the sum $(L + R)$ across all image pairs, matching or nonmatching, is $<L> + <R>$. Assuming left–right symmetry, such that monocular images are equally likely in either eye, we must have $<L> = <R>$. However, this means that the average value of $(L + R)$ is the same regardless of whether the images match. Note that this conclusion did not depend on the monocular computation being linear. L, R are often modeled as linear functions such as a weighted sum of photoreceptor activity across the image patch, but even if they were nonlinear, the same logic would hold.

False match: where similar left and right image-patches are wrongly classed as the same object, although more rigorous local correspondence would reveal that they differ

Even if we add a nonlinearity after binocular combination, $B = f(L + R)$, the neuron still does not implement strong correspondence, by the same logic as above. However, it can achieve weak correspondence, i.e., a higher average response for matching stimuli. Models of this form were originally proposed as models of binocular simple cells in the cat visual cortex (Ohzawa et al. 1990). The nonlinear function f can be as simple as a threshold, although models often include exponentiation as well.

Two possible routes to achieving strong correspondence have been proposed. One is to make the monocular computation extremely selective. In the limit where L, R are nonzero only for one possible image a, the distinction between weak and strong correspondence disappears. By making f a threshold at $1.5a$, for example, we can ensure that the neuron fires only when both eyes see the favored image a. Kral & Prete (2004) and Prete et al. (1996) proposed that this local correspondence via monocular feature detection is a possible mechanism for insect stereopsis. They postulated the existence of monocular neurons that are highly selective for the desired prey (in terms of contrast, speed, size, and retinal location) and a binocular neuron whose high threshold means that both monocular neurons must be active before it fires. Kral & Prete (2004, figure 3.15) did not consider this a form of stereopsis, arguing that this model "requires neither an explicit comparison of right and left retinal images nor a calculation of retinal disparity." However, since monocular neurons are "responsive only to prey-like stimuli. . .moving. . .at a particular speed" (Kral & Prete 2004, figure 3.15), and the binocular neuron fires only when both are active, the retinal images must both be similar to prey and thus at least somewhat similar to each other. Since the monocular neurons fire only when the prey is within the animal's acute zone, the binocular neuron is tuned to the disparity corresponding to the acute zones—explaining, for example, why mantids do not strike at stimuli whose vertical disparity would put one eye's image out of the acute zone. Of course, since this system depends on distinctive monocular features, it can only implement contour stereopsis. However, this would be sufficient for predators like praying mantids, toads, or cuttlefish, who use stereopsis to judge the absolute distance of moving prey against a stationary background. More recent evidence suggests that mantis stereoscopic neurons are not as highly selective as envisaged by Kral & Prete but that monocular processing nonetheless plays a critical role in simplifying correspondence (Nityananda et al. 2018, Rosner et al. 2019).

To achieve cyclopean stereopsis, mammals adopt an alternative approach. The process seems to begin with something like the $B = f(L + R)$ computation described above. Such neurons are only weakly selective, meaning that they respond to false matches when two different monocular images happen to elicit similar responses. However, many different binocular simple cells provide input into a single complex cell. The complex cells show stronger correspondence because image patches a, b, which elicit identical responses in one simple cell, will be discriminated by another simple cell. They also smooth out the monocular feature selectivity because different simple cells will be tuned to different features. It seems likely that this process is iterated several times across different cortical areas, combining information across orientations and scales (Parker 2007). By the time the information reaches the inferotemporal cortex, neurons have achieved strong local correspondence, with the responses to false matches all but eliminated (Cumming & DeAngelis 2001, Janssen et al. 2003, Parker 2007, Welchman 2016). It seems likely that this solution also involves global constraints mediated via long-range interactions, although little is known about the neural mechanisms.

This cascade model of binocular simple and complex cells was originally proposed for the cat cortex, was later applied to primates, and also seems to work well for the owl. The initial stage, weak local correspondence by binocular simple cells, also describes disparity-selective neurons in the mantis brain, at least for the sparse dataset available to date (Rosner et al. 2019, 2020). Thus, it seems that mammals, owls, and insects have all evolved the same basic building-block computation for local correspondence, although the monocular inputs differ. In mammals and owls, binocular simple cells operate on images defined by contrast, whereas in insects, there is an early stage resembling temporal high-pass filtering. Insect binocular simple cells thus operate on images defined by contrast change.

In primates, these binocular simple cells are just the start of a process spread across several brain areas, which ultimately achieves strong local correspondence and cyclopean stereopsis (Cumming & DeAngelis 2001, Parker 2007, Welchman 2016). At each level, there is a large population of neurons tuned to different disparities, determined by the location (and substructure) of their local receptive fields. This neural architecture is suitable for encoding a detailed map of disparity across a wide portion of the central visual field.

In insects, there are also half a dozen classes of disparity-tuned neurons spread across different brain areas (Rosner et al. 2019, 2020), but as yet, little is known about what computations they implement or whether insect stereopsis moves beyond weak local correspondence. It seems unlikely that praying mantis stereopsis encodes a map of disparity at anything approaching the 0.5° resolution of mantis eyes. The output may be encoded by just a few neurons, signaling the presence of prey within the area of space corresponding to their receptive fields.

STEREOPSIS AND FUSION WITHOUT LOCAL CORRESPONDENCE

Local correspondence has received a lot of attention in the literature, but it is not essential for usable binocular vision. As an example, consider a hypothetical creature whose lifestyle requires it to orient toward salient objects in its visual field, and suppose that the underlying neural circuitry is as shown in **Figure 12**. Monocular visual neurons, encoding the location of stimuli in each eye, excite binocular direction neurons in the central brain, which encode the angles through which to turn. These direction neurons compete with one another in a winner-take-all arrangement, and the animal turns through the angle encoded by the winner. For our hypothetical animal, the visual neurons are tuned to directions α apart (this could be the photoreceptor spacing or a coarser representation), and the binocular overlap is $\beta = 4\alpha$. In the monocular zone of each eye, monocular neurons are connected to just one central neuron. For example, an object in the monocular zone of the right eye, 3α to the right of straight ahead, initiates a turn rightward through angle 3α. Unless the object is infinitely distant, the animal will not be quite pointing directly at it after turning, but it will at least be closer than it was. In the binocular zone, the situation is more complicated. The appropriate action in response to an object α to the right of straight ahead in the left eye might be to turn rightward through α if the object is distant and also projects to α in the right eye, but it might be to maintain heading if the object is nearby and projects to $-\alpha$ in the right eye. The animal needs to compare information from the two eyes to orient correctly to objects in the binocular zone.

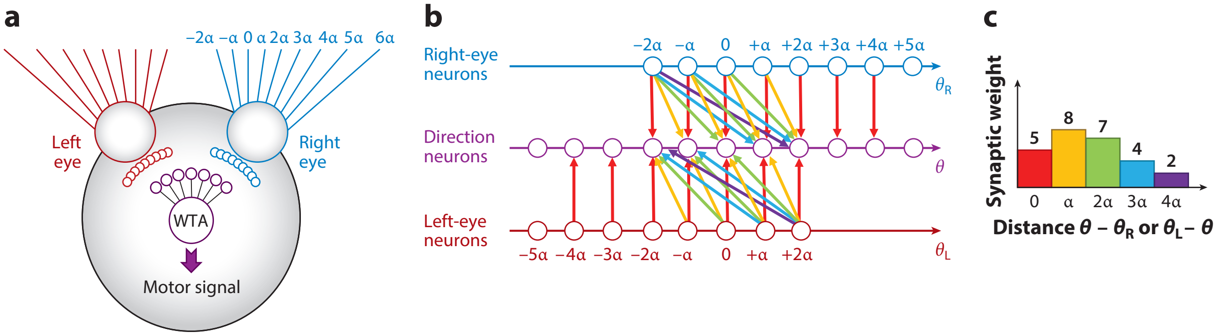


Figure 12

(*a*) Hypothetical nervous system. Monocular neurons are tuned to directions α apart in each eye. The binocular overlap is 4α. (*b*) Monocular neurons connect to binocular direction neurons. The color of each connection indicates its synaptic weight, which depends on (*c*) the difference between the neurons' preferred directions. Because this peaks at α for both eyes (*orange arrows*), the preferred disparity is 2α. A winner-take-all (WTA) computation means that the motor signal is set by whichever direction neuron is most active.

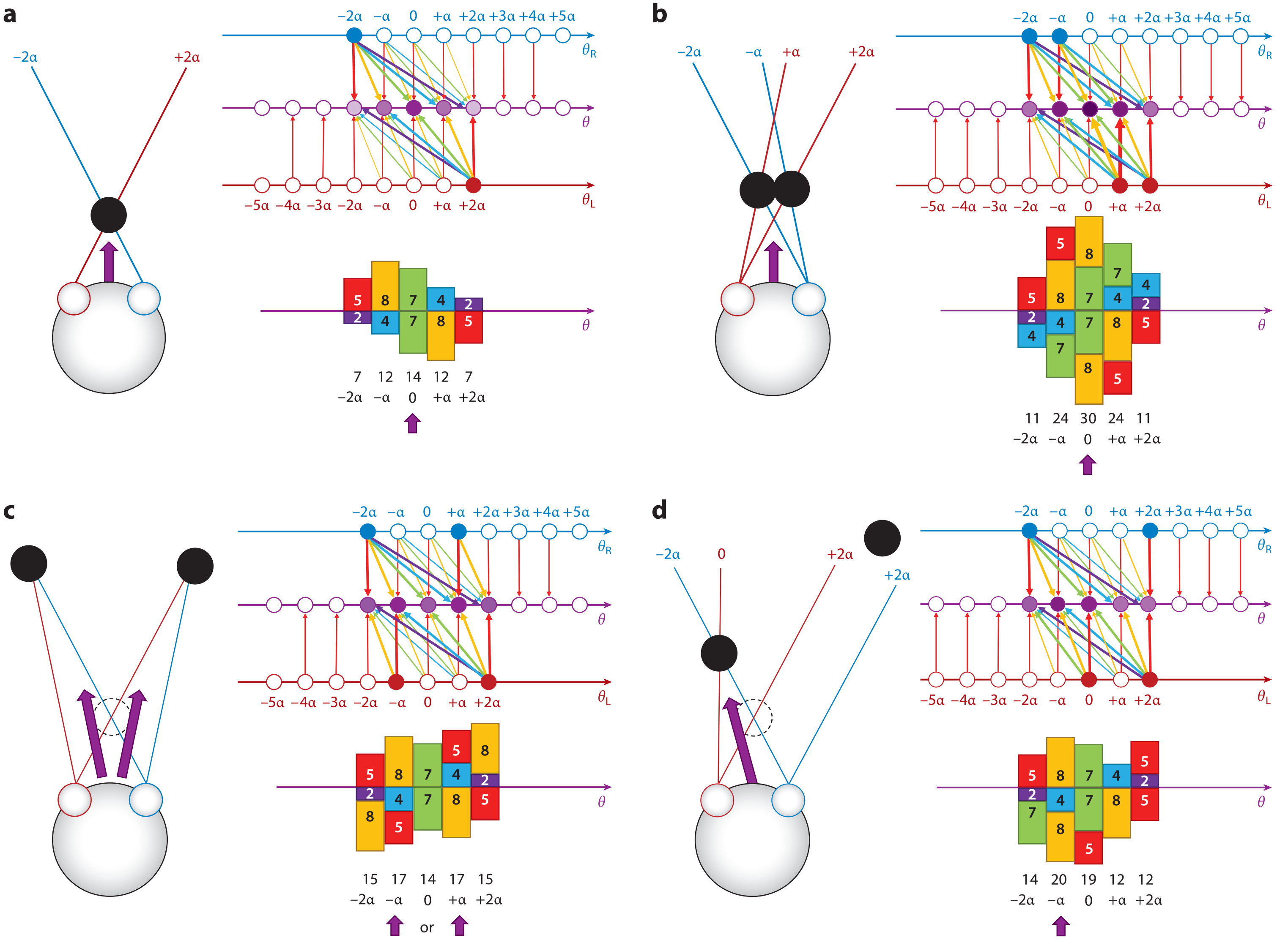
To achieve this, direction neurons in the binocular overlap receive input from both eyes. They sum inputs from left and right eyes with a synaptic weight. Critically, the synaptic weight depends on the distance between the preferred location of the monocular neuron and the preferred angle of the direction neuron. This incorporates a form of disparity tuning, with the preferred disparity being 2α. However, the direction neurons combine their monocular inputs purely linearly and thus do not implement even weak local correspondence.

This simple model can predict quite complex binocular orientation behavior. For example, views of one object straight ahead, or two nearby objects to either side of the midline (**Figure 13*a*,*b***), cause the animal to maintain heading, whereas views of two objects further apart on either side of the midline cause the animal to turn toward either one or the other (**Figure 13*c***; I assume that, if two direction neurons are equally strongly activated, then it is random which one wins). Furthermore, if there are two objects on either side of the midline, but one is much closer than the other, then the animal will turn towards the nearer object (**Figure 13*d***). This model agrees with observed behavior in the praying mantis, for example.

The animal behaves as if it has appropriately fused binocular direction signals for the object that it has selected. Moreover, it has a simple form of stereopsis, since it selects the nearer object in **Figure 13*d*** based solely on binocular disparity. The synaptic weighting tunes the direction neurons to disparity as well as direction; for example, the neuron that triggers orientation toward direction 0° responds more to an object at $\theta_{\mathrm{L}} = +\alpha$, $\theta_{\mathrm{R}} = -\alpha$ (disparity 2α) than to one at $\theta_{\mathrm{L}} = \theta_{\mathrm{R}} = 0$ (disparity 0), even though both have its preferred direction $\theta = 0°$.

Furthermore, unlike *Aeshna* (**Figure 11*d***), the animal behaves as if it solves the global correspondence problem. For example, it responds to a single object at $\theta_{\mathrm{L}} = +2\alpha$, $\theta_{\mathrm{R}} = -2\alpha$ as if it perceives an object on the midline (**Figure 13*a***), but when this stimulus is presented along with additional stimuli at $\theta_{\mathrm{L}} = -\alpha$, $\theta_{\mathrm{R}} = +\alpha$, as in **Figure 13*c***, the animal looks to either the left or right with equal probability, as if it perceives two objects—exactly like the global correspondence discussed in **Figure 11**.

Effectively, the winner-take-all nonlinearity provides a basic but workable form of global correspondence and fusion, despite the absence of local correspondence in previous processing stages. This model would not normally be considered a stereo vision algorithm because it does not produce a depth map across the scene. However, a depth map may not be needed to produce



(Caption appears on following page)

Figure 13 (*Figure appears on preceding page*)

How the hypothetical creature in **Figure 12** responds to four binocular stimuli. In each case, the monocular neurons receiving input are filled, and their synaptic connections are drawn in bold. The bar chart beneath shows the total synaptic input to the five binocular direction neurons; upper bars show input from the right eye, and lower bars show input from the left eye. The numbers below show the total input, and the blue arrow indicates the largest total. This is the winning direction, which controls the animal's response. (*a*) For a single close object on the midline, appearing at opposite directions in the two eyes, the animal looks along the midline, i.e., it shows binocular fusion. (*b*) Two nearby objects on either side of the midline are treated as a single object; again, the animal looks along the midline (as in mantids). (*c*) For two more distinct objects at the same distance, the animal is equally likely to turn toward either of them (slightly undershooting, as is also observed in mantids). (*d*) For two objects at different distances, the animal always turns toward the nearer object, i.e., it shows stereopsis. Note that, in panels *c* and *d*, the animal successfully ignores the ghost match (*dashed circle*) indicating an object on the midline, i.e., it shows global correspondence.

sensible binocular visual behavior. In the context of animal stereopsis, we need to expand our view to consider such algorithms and to discover whether they can successfully account for the full range of behavior.

CONCLUSIONS

Most animals, even those with laterally placed eyes, have at least some degree of binocular overlap. This may simply provide redundancy or limit a frontal blind zone; however, in recent years, it has become clear that many species also exploit their binocular overlap to derive depth information about their environment. This includes species like praying mantis, mouse, and cuttlefish, where such an ability was previously considered unlikely. Front-facing eyes, such as those of primates, may have evolved to permit high acuity in the frontal region, which in turn permits high stereoacuity, but the wide binocular overlap seems to have been retained for some other reason, such as a wide region of enhanced sensitivity. Primates seem to be unusual in committing to binocular oculomotor control; many mobile-eyed vertebrates are capable of switching between binocular and monocular oculomotor control.

Much of the literature around stereo correspondence, in psychology and neuroscience as well as in computer vision, is based on the premise that stereopsis produces a map of disparity across the visual field, implying a detailed solution of the stereo correspondence problem. Furthermore, the computational literature also generally assumes that stereopsis should work in arbitrary images, i.e., it should be cyclopean. In mammals and birds, this view seems to be correct. In a surprising example of convergent evolution, cyclopean stereopsis has been demonstrated in many mammals and birds. Cyclopean stereopsis depends on sophisticated stereo correspondence and can break camouflage in static images, revealing surface discontinuities, slant, and curvature. However, in other taxa, stereopsis may be very different. In amphibians, insects, and cephalopods, only contour stereopsis has been proved to date, since the tests used moving targets, where camouflage could be broken by early temporal filtering. In praying mantis, stereopsis seems to be supported by binocular computations similar to those implementing weak local correspondence in the mammalian cortex. Still simpler binocular behavior, such as orienting toward stimuli, may potentially be achieved without using local correspondence at all.

SUMMARY POINTS

1. Most animals have at least some binocular overlap, i.e., a region of space viewed by both eyes.

2. A binocular overlap offers several advantages, including redundancy, improved sensitivity, seeing around obstacles, and stereoscopic depth perception.
3. Stereopsis is not restricted to predators with frontal eyes, as has often been asserted, but is also found in prey animals with lateral eyes, such as mice and horses.
4. The precision of stereopsis reduces with distance, but it remains informative up to considerable distances (hundreds of meters in humans).
5. Solving stereo correspondence, i.e., figuring out which feature in the left eye matches up with which feature in the right, is a challenging computational problem that is often seen as essential for stereopsis. However, some species may gain useful stereoscopic information without achieving stereo correspondence.
6. In understanding the neural basis of stereopsis, it is useful to distinguish between neurons showing strong correspondence (higher response to images that match across the two eyes, after controlling for monocular response) and weak correspondence (higher response on average to matching images).
7. A key distinction is whether stereopsis works with features visible in each eye independently (contour stereopsis) or can work with arbitrary images to detect structure that is not visible in either eye (cyclopean stereopsis). (In the psychology literature, these are sometimes, rather misleadingly, referred to as local and global stereopsis.)
8. Different monocular inputs—for example, the pattern of light itself versus the rate at which light is changing—can produce very different results from similar stereo algorithms.

FUTURE ISSUES

1. What selection pressure led to binocular overlap in different species?
2. How widespread is stereopsis across taxa? How many times has it evolved?
3. Does cyclopean stereopsis exist outside of mammals and birds?
4. Do humans have distinct forms of stereopsis, e.g., for perception versus oculomotor control?
5. Do all species use the same fundamental building-block neural computation for stereopsis? Is cyclopean stereopsis achieved by combining more building blocks, or is it qualitatively different?
6. Do some species obtain useful stereoscopic information without achieving binocular fusion and/or stereo correspondence?

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