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Reply

Response to H.C. Howland, "Orbital orientation is not visual orientation"

We have hypothesized that the size of the binocular field among mammals has been selected to maximize the visually surveyable region around the animal (Changizi and Shimojo, 2008). At first glance it may seem that this hypothesis should always predict lateral pointing eyes, and a consequently small binocular field width. However, the hypothesis does not predict lateral pointing eyes in cases where the environment is filled with leafy occlusions and the animal's interpupillary distance surpasses the typical widths of the leaves (when both of these apply, we call the environment "cluttered"). In such cases, within an animal's binocular region the eyes tend to sample the scene independently. Laterally directed eyes also sample the scene independently, but the binocular region benefits from a variety of binocular summation, lowering the threshold for the recognition of objects in the binocular field. Our hypothesis predicts that mammals outside of leafy environments should have small binocular fields, independent of the size of the animal; but it predicts that for animals in leafy environments, whereas small animals should have small binocular fields (because their interpupillary distance is small compared to the typical occlusion width), large animals should have large binocular fields (because the binocular region begins to become more powerful at object recognition). Our paper provided evidence consistent with these predictions.

Howland's (2009) thoughtful comment raises issues with our paper. We begin our response by correcting several misunderstandings. First, it is not the case that, as Howland writes, we "predict that animals in non-cluttered environments and small animals whose intraocular distance is small relative to the "holes" in the clutter may retain more lateral pointing eyes". It is not the size of the "holes" that drives the optimal size binocular region for maximizing visual surveyability, but the size of the "leaves". Second, Howland writes, "A careful examination of these figures will show that in leafy environments the positive regression depends almost entirely on the primates, and in semi-leafy environments, upon the carnivora". The implication is that we did not communicate, or did not realize, that this is the case. However, in the article we explicitly point this out ourselves (p. 761), and we added a separate plot to emphasize it (Fig. 7). Our motivation for a plot confining the data to primates and carnivora (as well as artiodactyla) was that although our hypothesis predicts that binocular field width should increase as a function of body size for animals in leafy environments, our hypothesis currently lacks any means to predict the slope and y-intercept of the rise. It is probable that the specific nature of the rise depends on the taxon studied, in which case we expected that making the data more taxonomically homogeneous should reduce the variability, something that we found to be the case.

The thrust of Howland's argument is that orbital orientation is not visual orientation. He points out that for most mammals and virtually all primates, "both eyes gaze in the same direction with visual axes directed at the same point in space". He concludes, "Thus, while as the authors show, orbital convergence varies systematically with primate body size, optical convergence—the crucial factor in frontal vision—does not". But our hypothesis does not concern the evolution of visual orientation of mammals, i.e., the direction the eyes gaze in. Instead, our hypothesis concerns the size of the binocular region. Whereas carnivores and primates all have both eyes gazing in the same direction, their binocular field sizes vary considerably. For example, ferrets have binocular field widths of 80°, dogs have widths of about 100°, and humans have widths of about 140° (Heesy, 2004)—yet all have eyes which gaze at the same point in space. Animals with small binocular fields like ferrets have wider peripheral vision; and despite the ability for their eyes to face forward and fixate a point in space, each eye's medial visual field is more limited (usually terminating with a view of the muzzle). The central criticism of the commentary, as reflected in the commentary's title, appears to be due to a misunderstanding of our paper. We are partly responsible for this, because in our article's prose—and title—we often used the phrase "forward-facing eyes". We utilized it as a short-hand way of referring to cases where the entirety of the animal's visual field is shifted more toward the front; it is accordingly directly linked to binocular field width. However, it is easy to see now that "forward-facing eyes" could be misconstrued to mean "eyes that gaze at the same point in space".

Howland also argues that, although there is a strong correlation between binocular field size and orbital convergence across mammals (Heesy, 2004), the correlation among primates is not significant. However, among the 27 species from nine mammalian orders for which Heesy has overlap and convergence data, only six species are from primates, with little variation in orbital convergence (compared to the full 27 species data set). It is not surprising that the strong correlation across mammals is attenuated once the data are so drastically reduced in number and in data range. However, even so, there is an apparent trend among the six primates, and it is significant: $r = 0.737$, $p = 0.047$ (via a one-sided test). Furthermore, the primate data are not outliers when plotted amongst the full range of 27 species; the burden of evidence is consequently on the position that "primates are different" in regard to the existence of a correlation between binocular field size and orbital convergence. Howland then points out that the two lowest binocular field size primates of the six are nocturnal (bushbaby and tarsier), and, citing Walls (1967), suggests that, "to increase the brightness of the retinal image in nocturnal animals the lens is forced back into the eye, restricting the visual field, and hence the binocular field". However, no argument is given about the expected magnitude of a binocular field reduction on this basis; it is therefore unclear whether it could explain why, for example, Tarsier has a binocular field width

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that is 13° narrower than that of human, and nearly 20° narrow than that of squirrel monkey (from Heesy, 2004). Also, because the size of the binocular field depends on the medial limit of each eye's visual field, not the lateral limit, and because the medial border typically consists of the animal's muzzle (which is advantageous for visuo-motor feedback) (Changizi, 2009), nocturnality and axial length considerations are unlikely to much affect binocular field size. Furthermore, even if it were the case that these two primate species should not be included with the other four primates in the analysis of binocular field width versus orbital convergence, it would only argue that no conclusion about their relationship can be made given the remaining non-nocturnal primate data, because there would be far too few data, and an even smaller range of orbital convergence values. However, given that these remaining four data fall where they "ought" to on the overall mammalian plot of binocular field size versus orbital convergence, the default assumption should be that these primates are not different in this regard.

Howland puts forth an alternative hypothesis due to Walls (1967). He writes, "Carnivores that chase or pounce on prey have an obvious need for the distance estimation made possible by stereopsis". However, when in motion there are other cues for distance estimation that are often much more informative than stereopsis, including motion parallax (distance estimation is possible even when the motion is interocular, Shimojo et al., 1988); that carnivores are in "obvious need" for stereopsis (and to a greater extent than non-carnivores) is not clear. Even if carnivores benefit from stereopsis more than non-carnivores, this is different from arguing for a large binocular field, because stereopsis is found in the binocular field of mammals no matter the size. Presumably, the hypothesis is that a *larger* field of stereopsis is advantageous to carnivores. The fact that smaller carnivores have smaller binocular fields (and more lateral eyes) is a prima facie counterargument to this; these small binocular field animals are highly efficient hunters. Howland hypothesizes that such animals have small binocular fields only because they are small, and at risk of predation from larger predators. There are, however, many non-carnivore predators at little or no risk of predation that get by with a small binocular region, such as sharks, large reptiles, large predator dinosaurs, most birds, and cetaceans. It is also not sufficient to explain why the largest binocular regions are found on primates. Stereoscopy is, prima facie, least effective for large animals in highly leafy environments because, in such situations, each eye's view within the binocular region tends to see different parts of the scene than the other eye, making disparity-based stereoscopy handicapped; yet it is exactly in these "cluttered" scenarios that one finds the largest binocular fields. Finally, even with a good argument for the advantage of a large stereoscopic binocular region, any theory must explain why these advantages are worth the cost of the loss of vision in the periphery.

The commentary by Howland ends by mentioning several other hypotheses (together amounting to what may be called the "conventional view") that he suggests explain the phenomena. He describes the conventional view as follows: "…that the evolutionary persistence of periscopy is due to the forces of predation in open and semi-open environments, and that, where these forces are relieved, the great advantages of stereopsis in distance estimation and uncovering camouflage, together with those of increase of signal to noise ratio of binocular summation". The unparsimonious nature of the conventional view—it consists of layered mix of multiple sub-hypotheses—makes it difficult to theorize about and test. In contrast, our "X-ray" hypothesis is simple, relying only on the desideratum that animals should evolve to "see the most" with their two eyes.

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Mark Changizi *
Department of Cognitive Science, Rensselaer Polytechnic Institute, Troy, NY 12180, USA
E-mail address: changizi@rpi.edu

Shinsuke Shimojo
Division of Biology, MC 139-74, Caltech, Pasadena, CA 91125, USA

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* Corresponding author. Tel.: +1 518 276 3788.