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Peter Neri

JN 93:1823-1826, 2005. doi:10.1152/jn.01068.2004

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A Stereoscopic Look at Visual Cortex

Peter Neri

School of Optometry, University of California, Berkeley, California

Submitted 12 October 2004; accepted in final form 18 November 2004

Three recent studies offer new insights into the way visual cortex handles binocular disparity signals. Two of these studies recorded from single neurons in two different visual areas of the monkey brain, one (V5/MT) in dorsal and one (V4) in ventral cortex. While V5/MT neurons respond similarly to neurons in primary visual cortex (V1), V4 neurons appear to reflect a more advanced stage in the analysis of retinal disparity, closer to the perceptual experience of stereoscopic depth. Both studies are consistent with a third study using fMRI to address similar questions in humans. Together with previous evidence, these results suggest a new framework for understanding stereoscopic processing based on the separation between ventral and dorsal streams in visual cortex.

Humans, like many other animals, possess two eyes that are frontally placed and can thus simultaneously inspect the same region of visual space. Objects within this overlapping region project slightly disparate images to the two retinæ. Our brain uses these retinal disparities to infer the distance of objects, to guide our fixational eye movements, and to provide us with the perception of stereoscopic depth. This important phenomenon was not discovered until the beginning of the 19th century (Wheatstone 1838), and it was only in the 1960s that neurons in cat V1 were shown to respond selectively to retinal disparity (Barlow et al. 1967; Nikara et al. 1968). It was hypothesized that these neurons carry the signals used by the brain to support stereoscopic vision. These results were subsequently confirmed in monkeys (Poggio 1995) and other animals (Pettigrew 1980).

Although many neurons in V1 respond selectively to retinal disparity, and retinal disparity certainly plays a central role in stereoscopic perception, it turns out that the selectivity of these neurons differs markedly from the selectivity experienced by humans in stereoscopic perception, suggesting that V1 is only part of the story (Parker 2004). There are two major differences, outlined in the following text.

The first difference has to do with absolute versus relative disparity. The absolute disparity of an object is determined by the differences in the two retinal images generated by that object alone. These differences are measured with reference to the coordinate system of the two retinæ. The retinal coordinate system, however, depends on where the eyes fixate, meaning that the absolute disparity of an object is not unique but varies all the time as we change our fixation. The relative disparity between two objects is the difference between the absolute disparity of one object and that of the other object. This

measure is more robust in that it does not depend on where we look: as the eyes verge in and out to change fixation, both absolute disparities change, but their difference remains constant. Humans are especially sensitive to relative disparity, much less to absolute (Westheimer 1979). Moreover, large changes in absolute (but not relative) disparities can go unnoticed (Erkelens and Collewijn 1985). In stark contrast to these perceptual observations, neurons in primary visual cortex are selective for absolute not for relative disparities (Cumming and Parker 1999), providing the first piece of evidence that further processing downstream of V1 must be happening.

The second difference has to do with correlated versus anticorrelated random-dot stereograms [random arrays of dots that look unstructured when viewed monocularly, but yield disparity-defined structure under binocular inspection (Julesz 1971)]. With random-dot stereograms (RDSs), the task of correctly matching one dot in the left eye with its counterpart in the right eye can be a challenging one for our visual system, particularly when dot density is high and despite corresponding dots having the same contrast in both eyes (i.e., their being contrast-correlated, white-matching-white and black-matching-black). If the contrast of the image in one eye is reversed (i.e., black dots are turned white, and white dots are turned black, generating an anti-correlated RDS), the matching mechanism breaks down and humans do not experience a sense of stereoscopic depth (Cogan et al. 1995; Cumming et al. 1998). This is in contrast with the properties of V1 neurons that respond to both types of RDSs rather than discarding the anti-correlated type (Cumming and Parker 1997). In particular, V1 neurons respond to anti-correlated patterns in a manner predicted by a widely accepted energy model of how these neurons detect retinal disparities (Ohzawa et al. 1990).

The conclusion from the studies cited so far is that the final stages of stereoscopic processing must reside somewhere outside primary visual cortex (Parker 2004). The question is, of course, where. This question has been the subject of intense research over the past 10 yr, and very recent results appear to provide a preliminary, unexpected answer.

Some neurons in the cortical area immediately after V1 in the visual system, area V2, show selectivity for relative disparity (Thomas et al. 2002). This is encouraging because it confirms our expectation that signals downstream of V1 would be more similar to what we perceive. However, the coding of absolute and relative disparity in V2 is not as markedly different from V1 as one would hope. The next area is V3. There is only one study that provides some relevant information about V3 (Poggio et al. 1988), and it indicates that V3 neurons respond to anti-correlated RDSs in a manner similar to V1 neurons. It must be noted that this study does not provide conclusive evidence in this respect because it makes no clear

Address for reprint requests and other correspondence: School of Optometry, University of California, Berkeley, CA 94720-2020. (E-mail: pn@white.stanford.edu).

distinction between anticorrelated and uncorrelated RDSs and only examined sensitivity at zero disparity, so the question remains open in V3. After this area, the visual system takes two different directions: dorsally toward V3A, V7 (in humans), V5/MT and MST, and ventrally toward V4, V8 (in humans) and IT (Fig. 1). Which direction to go?

Given previous evidence on the role of macaque V5/MT in stereoscopic processing (Bradley et al. 1998; DeAngelis et al. 1998; Dodd et al. 2001), the dorsal stream seemed an obvious bet. This also made sense in the context of fMRI experiments showing that human V3A is particularly responsive to a pair of disparity planes defined by RDSs (Backus et al. 2001). There are three main lines of evidence in support of a role for V5/MT in stereoscopic perception: comparison between neuronal and behavioral sensitivity, choice probability, and microstimulation experiments. A good match between neuronal and behavioral performance has been demonstrated in both V5/MT (Uka and DeAngelis 2003) and V1 (Prince et al. 2000). These studies provide evidence that signals in either V1 or V5/MT (or both) have the potential to support perception in certain stereojudgement tasks but not that they actually do. More convincing evidence in this direction comes from studies demonstrating that the activity of single neurons in V5/MT allows one to predict the choice that the animal will make on a given trial with a (choice) probability greater than chance (Dodd et al. 2001; Uka and DeAngelis 2004). The general problem with studies using choice probability is that they provide correlational not causal evidence. More specifically, it is difficult to rule out feedback from other areas as a potential source for the correlation, even when taking great care to exclude this possibility (Uka and DeAngelis 2004). The most direct evidence therefore comes from microstimulation studies. DeAngelis et al. (1998) have shown that targeted microstimulation of disparity-selective columns in V5/MT can bias the monkey's judgement in a far-near stereo task that relies on absolute disparity. However, when microstimulation of V5/MT is performed in the context of perceptual judgements that are based on relative disparity, no effect is observed (G. C. DeAngelis, personal communication). The difference just mentioned urges

us to consider that, as already discussed by this and other authors (Neri et al. 2004; Parker 2004), the perceptual distinction between absolute and relative disparities is not clear-cut. Absolute disparities can in fact support stereo-judgement tasks, although at a much coarser scale than relative disparities (Westheimer 1979). It is therefore possible that absolute disparity signals in V5/MT and in the dorsal stream, as well as controlling vergence, may be involved in coarse perceptual stereo judgements that do not require the processing of relative disparity. One last result that is worth mentioning in this context is a study showing that V5/MT neurons are often selective for slant across changes in mean disparity (Nguyenkim and DeAngelis 2003), therefore suggesting that they may have the ability to code for relative disparity. However, the type of slant selectivity observed by Nguyenkim and DeAngelis (2003) is not entirely robust to changes in mean disparity, and these authors interpret most of their results as deriving from differences in the selectivity to absolute disparity across the receptive field. A receptive field with heterogeneous selectivity to absolute disparity will display some degree of selectivity for relative disparity, but true relative disparity selectivity is assessed more explicitly with an experimental protocol like that of Thomas et al. (2002) in which responses to relative disparity were assessed over a wide range of absolute disparities. Using this protocol, Uka and DeAngelis (2002a) have shown that V5/MT neurons do not code for relative disparity. In summary, although there is evidence for the involvement of V5/MT in some stereo tasks, there is now a growing number of studies indicating that V5/MT neurons do not directly support some important and strictly perceptual aspects of stereovision (see also Christiansen et al. 2004). It should also be emphasized that the availability of a large number of studies on V5/MT may not reflect the actual impact of this area's contribution to binocular processing but rather a trend in the stereo-community that may soon change.

Despite all the preceding unresolved issues relating to which aspects of stereoscopic perception are supported by V5/MT neurons (a topic that clearly requires further investigation), the evidence in favor of a role for the ventral stream in stereo-

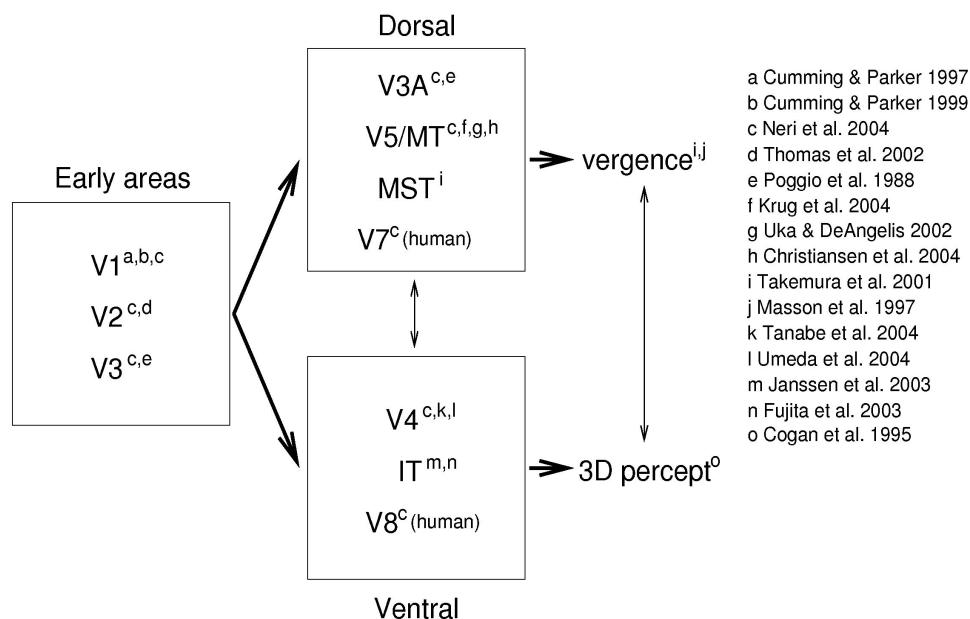


FIG. 1. Summary of the literature on the neural basis of stereoscopic motor and perceptual processing, organized according to (respectively) dorsal and ventral streams in visual cortex (Milner and Goodale 1992). This framework is likely to suffer from oversimplification but successfully brings together most of the available literature on this topic. Studies c, f, and k are the focus of this review. Smaller arrows are intended to warn readers against interpreting the dorsal/ventral distinction too rigidly as the 2 modules interact extensively. Areas V7 and V8 have been identified in humans, but a direct homologue mapping in monkey cortex has not been established.

scopic perception seemed too limited to grant attention as a potential alternative. This evidence mainly came from one published study (Janssen et al. 2003) demonstrating that neurons in macaque IT discard anti-correlated signals and from a preliminary report (Fujita et al. 2003) that signals in IT show high choice probabilities in a fine stereoacuity task. However, IT [being a terminal station in the ventral stream (Felleman and Van Essen 1991)] is far removed from the early areas (V1–V3) and receives extensive inputs from the dorsal stream (Baizer et al. 1991; Saleem et al. 2000), leaving open the possibility that the relevant processing is happening in dorsal cortex and is later relayed to ventral cortex.

Three very recent papers now provide us with a clearer picture. They indicate that, rather unexpectedly, the processing supporting stereoscopic perception is likely to be completed in the ventral stream. The first study (Krug et al. 2004) recorded from neurons in macaque V5/MT and tested their responses to correlated and anticorrelated RDSs. The authors show that V5/MT neurons, like MST neurons (Takemura et al. 2001), respond to both types of RDSs in a way that is similar to V1 neurons. This paper appears in the *Journal of Neurophysiology* together with an fMRI study of selectivity for absolute and relative disparity in human visual cortex (Neri et al. 2004) that relied on a fMR-adaptation technique designed to target neuronal selectivity at the subpopulation level (Grill-Spector and Malach 2001). The fMRI results indicate that the dorsal stream is primarily involved with processing absolute disparity, whereas areas in the ventral stream show a significant degree of selectivity for relative disparity. These two studies are therefore consistent in providing evidence that signals in the dorsal stream do not directly support the final stages of stereoscopic perception. The fMRI study, moreover, is consistent with the already cited IT study (Janssen et al. 2003) in showing that the ventral stream may be a better candidate. Given these various indications, one would like to see what neurons do in an early area along the ventral stream. This piece of information now comes from a study by Tanabe et al. (2004), who show that neurons in V4 (the earliest area in the ventral stream) show a noticeable degree of exclusion for anti-correlated RDSs, significantly more pronounced than in V1. Moreover, recent results from the same group show that V4 neurons are remarkably selective for relative disparity (Umeda et al. 2004). The quantitative difference in the response to anti-correlated RDSs between V4 (Tanabe et al. 2004) and V1 (Cumming and Parker 1997) is clearly significant, but it should not be overstated in that it is relatively small and the two studies are not directly comparable [in particular, Tanabe et al. used stimuli of very low luminance (1.5 cd/m²), possibly compromising stereovision]. Rather, the V4 result should be combined with the earlier results in IT (Fujita et al. 2003; Janssen et al. 2003). Taken together, this evidence is clearly pointing toward an important role for the ventral stream in stereoscopic perception.

The picture that is emerging from these studies fits nicely with current theories on the dorsal/ventral dichotomy in visual processing. Ventral cortex is believed to support perceptually relevant signals, whereas dorsal cortex is believed to process visual information of immediate relevance to motor responses (Milner and Goodale 1992). In the specific context of stereoscopic vision, motor processing is mostly related to vergence eye movements, which allow the two eyes to change fixation by rotating inward or outward. Absolute disparity signals are of

obvious importance to vergence control, and vergence eye movements are driven by anti-correlated RDSs in a manner that is consistent with the response of V1 and MST neurons (Masson et al. 1997; Takemura et al. 2001). In other words, the motor side of stereoscopic processing displays characteristics that are easy to reconcile with the signals that have been measured along the dorsal stream.

In the same way that (as discussed in relation to the V5/MT literature) the perceptual compartmentalization of absolute and relative disparities is not water-tight and is only viable to a limited extent, the dorsal/ventral separation discussed so far is to be intended as a rough architectural distinction rather than a rigid dichotomy (Maunsell 1992). Behavior tells us that perception influences action, and action influences perception, so it is certainly simplistic to imagine that the two would be happening in isolation from each other in two different parts of the brain. Depending on task demands, quality of the available signals, required speed of response and other parameters that determine the performance of the observer, different cortical modules may display different degrees of involvement in different aspects of behavior (Fias et al. 2002). Even if it became possible to identify clear specializations, caution should be used in comparing modules across processing streams: is it really correct, for example, to rank V4 and V5/MT at similar stages within their respective hierarchies in the ventral and dorsal streams? This rather arbitrary comparison, although in line with current literature (Felleman and Van Essen 1991), may turn out to be more problematic than expected. Nevertheless, despite the obvious limitations of such an oversimplified description, the dorsal/ventral framework described in this article does an excellent job of bringing together a dozen available studies on the topic (see Fig. 1), and similar ideas have already been proposed by other authors (Parker 2004; Tyler 1990).

It is remarkable how much was learnt about stereoscopic processing over the past 10–15 yr. We now know that the energy model provides an adequate description of the earliest stage in disparity processing (Ohzawa 1998). This model will need to be modified in its details (Cumming 2002; Read and Cumming 2003, 2004; Read et al. 2002; Uka and DeAngelis 2002b), but the main features are likely to be correct. The new findings reviewed in this article offer a preliminary picture of what happens after this initial stage. They indicate that early disparity signals may be channeled in two directions: toward the dorsal stream to provide guidance to the vergence motor system and possibly support coarse stereo judgements; and toward the ventral stream, where they would undergo further analysis to establish a richer perceptual representation of surface structure and possibly of the detailed three-dimensional arrangement of objects in space. Further research will be necessary to confirm whether this simple framework gets anywhere close to providing a veridical description of stereoscopic processing in visual cortex.

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