

these experiments suggest, may have distinct properties. The data presented here suggest that the presence of a second pacemaker (the DN1) fortifies the network, allowing behavioral rhythms to persist under conditions that would suppress individual oscillators. The network organization of the fly circadian pacemaker, and that of mammals, is likely critical to maintain rhythms under a variety of environmental conditions, such as different seasons. Given the potential importance of rhythms in health and disease, this is no small feat.

REFERENCES

- Busza, A., Emery-Le, M., Rosbash, M., and Emery, P. (2004). *Science* 304, 1503–1506.
- Emery, P., Stanewsky, R., Hall, J.C., and Rosbash, M. (2000a). *Nature* 404, 456–457.
- Emery, P., Stanewsky, R., Helfrich-Forster, C., Emery-Le, M., Hall, J.C., and Rosbash, M. (2000b). *Neuron* 26, 493–504.
- Grima, B., Chelot, E., Xia, R., and Rouyer, F. (2004). *Nature* 431, 869–873.
- Hardin, P.E. (2005). *Curr. Biol.* 15, R714–R722.
- Helfrich-Forster, C. (2005). *Genes Brain Behav.* 4, 65–76.
- Klarsfeld, A., Malpel, S., Michard-Vanhee, C., Picot, M., Chelot, E., and Rouyer, F. (2004). *J. Neurosci.* 24, 1468–1477.
- Murad, A., Emery-Le, M., and Emery, P. (2007). *Neuron* 53, this issue, 689–701.
- Renn, S.C., Park, J.H., Rosbash, M., Hall, J.C., and Taghert, P.H. (1999). *Cell* 99, 791–802.
- Stoleru, D., Peng, Y., Agosto, J., and Rosbash, M. (2004). *Nature* 431, 862–868.
- Stoleru, D., Peng, Y., Nawathean, P., and Rosbash, M. (2005). *Nature* 438, 238–242.
- Yoshii, T., Funada, Y., Ibuki-Ishibashi, T., Matsumoto, A., Tanimura, T., and Tomioka, K. (2004). *J. Insect Physiol.* 50, 479–488.

Reconstructing the World: Switching from Segmentation to Integration Allows Neurons in Area MT to Make “Sense” of the Visual Scene

Alexander Thiele^{1,*}

¹School of Biology and Psychology, Newcastle University, Framlington Place, Henry Wellcome Building, Newcastle upon Tyne NE2 4HH, United Kingdom

*Correspondence: alex.thiele@ncl.ac.uk

DOI 10.1016/j.neuron.2007.02.008

Huang et al. in this issue of *Neuron* show that primate area MT neurons exploit contextual cues to adequately interpret motion information. MT neurons switch from segmentation to integration when motion arises from single rather than multiple objects. This switching may help solve the aperture problem and bind distant object components into a perceptual whole.

The visual world, as projected onto our retinas, is fraught with continuously changing ambiguous signals. The brain is faced with the formidable challenge of extracting meaning from these signals and generating an image of the external world that contains the information necessary for survival. In the process, the external world is *reconstructed* from the two-dimensional, unstable and moving input from the retina, where detail is signaled by millions of neurons that view the world through small “windows”: their receptive fields. Although signals from these receptive fields are pooled at subsequent stages of visual processing, neurons in mid-level visual

areas still suffer from “seeing” only a restricted part of the visual world, a phenomenon which results in the so-called aperture problem (Wallach, 1935). This problem arises if a moving contour is viewed through an aperture (Figure 1B). Under those circumstances, motion direction and speed are impossible to determine unless additional information is provided. Since every individual neuron has a limited window to the world, it is regularly confronted with this problem. In order to overcome it and assign appropriate meaning to object parts within these apertures, the content within must be appropriately influenced by the content without—vision is hence an act

of interpretation, whereby segments of the visual scene are interpreted in light of the larger context within which they appear. Fortunately, objects and scenes often occur and move in statistically predictable ways in our visual environment. Consequently, the visual system frequently has “reason to believe” that a particular feature is present at a particular location, because of the spatial structure of the current scene, the temporal structure of its evolution over time, and prior knowledge of the spatiotemporal structure of the visual world (Kersten et al., 1996). Vision as an act of integration and interpretation is exemplified in Figure 1A. The artist has painted 2D

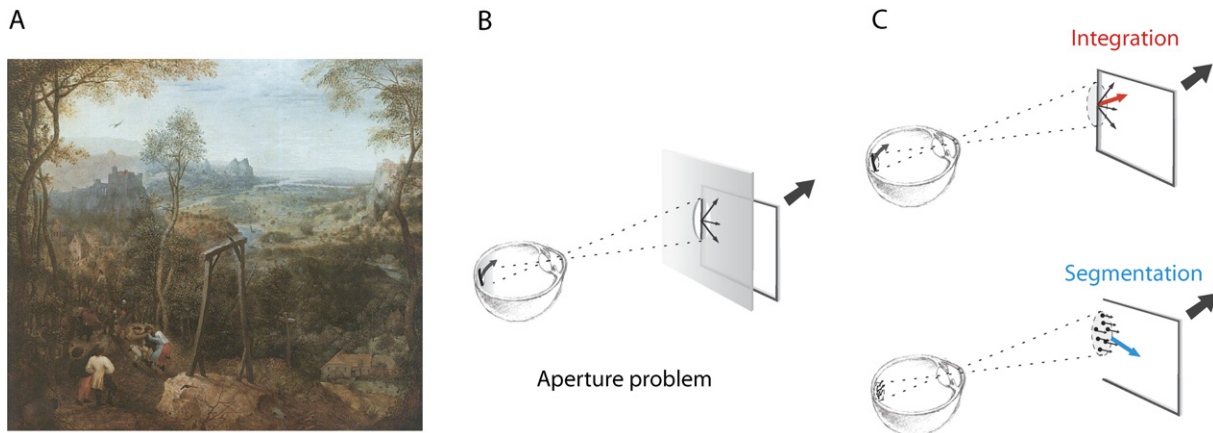


Figure 1. Spatial Integration and the Aperture Problem

(A) *Magpie on the Gallow* by Breugel, Pieter the Elder. The painting illustrates the necessity to integrate information from different spatial locations to “make sense” of the visual input. While every local part of the gallow is adequately depicted, the overall configuration is violating the geometric laws of pictorial representation from 3D to 2D space. Spatial integration is thus required to determine the improbability of the spatial configuration, i.e., to interpret the visual image. “Interpretation” is a substantial computational challenge for individual neurons. Due to their restricted receptive field size, they face the “aperture problem” (B). The aperture problem states that motion direction of an isolated contour seen through an aperture is effectively undetermined. The contour inside the aperture could move very fast to the upper left (or lower right) or move much slower to the right. Additional information through spatial integration is thus required to adequately resolve the direction of motion.

(C) Huang et al. (2007) have demonstrated that neurons in MT engage in motion integration, when motion inside the receptive field is part of a coherently moving object that extends well beyond the receptive field. Although the motion direction inside the receptive field is undetermined (the aperture problem), the information from the nonclassical receptive field is integrated such that the “true” motion direction of the object is largely recovered (red arrow). If, however, motion within the classical receptive field and motion outside the classical receptive field arise from separate objects, neurons engage in segmentation, whereby the motion contrast between the two objects is enhanced (blue arrow).

constellations that violate the rules of perspective, obviously so in terms of the gallow. However, the violation is only apparent when information from different parts of the image is integrated. Integration is necessary because each local segment of the gallow conforms to the geometric laws of pictorial representation—and still the sum of the local segments yields an unlikely geometric object.

Individual neurons are faced with a comparable problem. They have to receive information from extended parts of a visual scene to “make sense” of the local information that is present inside their receptive field. This information is provided by the nonclassical receptive field (nCRF), a part of visual space where stimuli do not directly yield cell responses but influence the processing of stimuli that occur inside the classical receptive field (CRF). nCRF influences have been widely studied in a variety of different feature domains (e.g., color, orientation, motion) and were found to be effective in all of them (Albright and Stoner, 2002). Interestingly, influences from the nCRF were found to

be mostly antagonistic, whereby contrasting information outside the CRF enhances the response to the information present inside the CRF, a mechanism that supports scene segmentation. In the motion domain, such antagonism enhances the difference between objects that move in different directions. However, when the stimulus motion inside the receptive field is ambiguous, i.e., when there is an aperture problem, such antagonism will result in a systematic misrepresentation of direction. Mechanisms of segmentation should coexist with mechanisms of integration. When a coherent object moves in a specific direction, then moving parts of the object outside the CRF should support the appropriate interpretation of the parts that move within the CRF. By means of such integration the aperture problem could effectively be overcome.

An elegant study in this issue of *Neuron* (Huang et al., 2007) demonstrates that motion-selective neurons from the middle temporal area (MT) of the primate visual cortex are able to solve the aperture problem and that they also switch from segmentation to integra-

tion, depending on the specific stimulus configuration. The authors placed an elongated contour, which was part of a square (Figure 1C) inside the CRFs of area MT neurons. The square was then moved in four different directions. By definition, the motion direction of the elongated contour within the CRF (the aperture) was ambiguous. If the nCRF acted antagonistically, the neuron should signal a direction of motion that is systematically deviated from the global motion of the square. If, however, the nCRF stimulation gave rise to integration, the neurons should signal a direction of motion in line with the global motion of the square. Under these stimulus conditions, most of the neurons in Huang et al.’s (2007) study engaged in integration, not segmentation. This is an important finding on its own, as most previous studies failed to show integration of information from the nCRF (but see e.g., Li et al. [2006]). To further determine whether neurons can switch from segmentation to integration, the authors changed their stimulus configuration. Now, they displayed a patch of coherently moving dots inside the receptive field (which provided

unambiguous motion information) while still presenting most of the square in the nCRF (Figure 1C). Since motion inside the CRF and outside the CRF was now generated by separate objects, segmentation mechanisms should be activated. The authors found indeed that the same neurons, which previously engaged in motion integration, now switched to segmentation, i.e., under these stimulus conditions, the surround acted antagonistically. The study demonstrates that surround modulation is not obligatorily antagonistic—it is stimulus specific. This nicely shows that neurons adapt to the computational problems they are facing, and they do so on very short time scales. It also demonstrates that neuronal properties established with a specific stimulus class do not necessarily generalize.

Future studies will have to determine whether this context-dependent switching generalizes to other classes of stimuli. It is likely that the phenomenon generalizes to stimuli where the depth plane within which they appear is systematically manipulated. Previous studies in primate V1 (Sugita, 1999) and V2 (Bakin et al., 2000) have demonstrated that neurons engage in completion of illusory figures (a form of integration) when the context is appropriate for such an interpretation. Additional studies will also have to determine the spatial limits of the surround influences and investigate whether segmentation and integration mechanisms have a similar spatial

reach. Another important question for future research is whether the phenomenon is contrast invariant. Previous research has demonstrated that suppressive (antagonistic) mechanisms are dominant at high contrast, while integration mechanisms are enhanced at low stimulus contrast (Polat et al., 1998). This intuitively makes sense, as redundancy should be reduced at high contrast while sensitivity should be increased at low contrast. But if integration is dominant at low contrast, segmentation mechanisms may suffer with the possible consequence of scene misinterpretation.

The ultimate challenge will be to understand the microscopic mechanisms that mediate this flexible implementation of stimulus-dependent switching between segmentation and integration. A recent study has demonstrated that cholinergic mechanisms can regulate spatial integration in V1 (Roberts et al., 2005) Although this is a first step toward understanding the mechanisms of spatial integration, the effects described in the study by Huang et al. (2007) are bound to be mediated by a complex interaction between inhibitory, excitatory, and neuromodulator interactions (Zinke et al., 2006) within area MT, probably aided by input from other cortical areas. Feedback signals from “higher” areas may contribute to the switching from segmentation to integration if “automatic” object-based attention mechanisms are activated (Mitchell et al.,

2004; Muller and Kleinschmidt, 2003). To reveal these interactions in detail is an exciting challenge for systems neuroscience. Ultimately, we may obtain a detailed picture of how the brain reconstructs the external world at the micromechanistic, neuronal, and perceptual level, and such a picture will be well worth the effort.

REFERENCES

- Albright, T.D., and Stoner, G.R. (2002). *Annu. Rev. Neurosci.* 25, 339–379.
- Bakin, J.S., Nakayama, K., and Gilbert, C.D. (2000). *J. Neurosci.* 20, 8188–8198.
- Huang, X., Albright, T.D., and Stoner, G.R. (2007). *Neuron* 53, this issue, 761–770.
- Kersten, D., Knill, D.C., Mamassian, P., and Bühlhoff, I. (1996). *Nature* 379, 31.
- Li, W., Piech, V., and Gilbert, C.D. (2006). *Neuron* 50, 951–962.
- Mitchell, J.F., Stoner, G.R., and Reynolds, J.H. (2004). *Nature* 429, 410–413.
- Muller, N.G., and Kleinschmidt, A. (2003). *Neurosci.* 23, 9812–9816.
- Polat, U., Mizobe, K., Pettet, M.W., Kasamatsu, T., and Norcia, A.M. (1998). *Nature* 391, 580–584.
- Roberts, M.J., Zinke, W., Guo, K., Robertson, R., McDonald, J.S., and Thiele, A. (2005). *J. Neurophysiol.* 93, 2062–2072.
- Sugita, Y. (1999). *Nature* 401, 269–272.
- Wallach, H. (1935). *Psychol. Forsch.* 20, 325–380.
- Zinke, W., Roberts, M.J., Guo, K., McDonald, J.S., Robertson, R., and Thiele, A. (2006). *Eur. J. Neurosci.* 24, 314–328.