

## TOPICAL REVIEW

# Recounting the impact of Hubel and Wiesel

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David Hubel and Torsten Wiesel provided a quantum step in our understanding of the visual system. In this commemoration of the 50th year of their initial publication, I would like to examine two aspects of the impact of their work. First, from the viewpoint of those interested in the relation of brain to behaviour, I recount why their initial experiments produced such an immediate impact. Hubel and Wiesel's work appeared against a background of substantial behavioural knowledge about visual perception, a growing desire to know the underlying brain mechanisms for this perception, and an abysmal lack of physiological information about the neurons in visual cortex that might underlie these mechanisms. Their initial results showed both the transformations that occur from one level of processing to the next and how a sequence of these transformations might lead to at least the elements of pattern perception. Their experiments immediately provided a structure for conceptualizing how cortical neurons could be organized to produce perception. A second impact of Hubel and Wiesel's work has been the multiple paths of research they blazed. I comment here on just one of these paths, the analysis of visual cortex in the monkey, particularly in the awake monkey. This direction has led to an explosion in the number of investigations of cortical areas beyond striate cortex and has addressed more complex behavioural questions, but it has evolved from the approach to neuronal processing pioneered by Hubel and Wiesel.

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David Hubel and Torsten Wiesel illuminated our understanding of the visual system with experiments extending over some 25 years, but it all began with their initial report (Hubel & Wiesel, 1959), which this issue of *The Journal of Physiology* commemorates. This initial report and the subsequent extension in 1962 (Hubel & Wiesel, 1962) were landmarks in exploring how neurons in the brain could be organized to produce visual perception. As a psychology graduate student at that time, this insight into how neurons in the brain could be organized to produce behaviour was riveting. What I would like to recount first is why their initial experiments produced such an impact at the time, and while this is an unabashedly personal view, I suspect it is not a unique one.

A second impact of Hubel and Wiesel's work results from the multiple trails of research they blazed. After starting with the sequence of visual processing in cat cortex, they relentlessly extended this to include such directions as the columnar organization of cortex underlying this processing, the differential response to wavelengths of light, the identification of ocular dominance, the development of that dominance, and the neuronal

organization in the monkey. I would like to comment on just the last of these directions because I have the greatest familiarity with it. Specifically, I would like to relate their work to the explosion of work in awake monkeys that I think has evolved from the analysis of neuronal processing pioneered by Hubel and Wiesel.

## Initial findings in striate cortex: the right results at the right time

The view from Hubel and Wiesel's perspective has been candidly documented (Hubel, 1982; Hubel & Wiesel, 2005) so that what I consider is the impact of their work from the viewpoint of an interested outsider. My continuing impression is that the major interest in Hubel and Wiesel's initial reports came from those interested in vision and visually guided behaviour. While I refer to them as psychologists, which I believe they predominantly were, this should be taken as shorthand for all those across a variety of fields who were interested in behaviour. Over a short period of time their work became the centre of most investigations into visual processing in the cat and then

the monkey. Their names became such a brand name that H&W rolled off the tongue as easily in the lab as A&W root beer did at lunch.

The excitement over their experiments can be better appreciated by considering the intersection of the knowledge accumulated about visual perception by the time of their discoveries, the latent interest in the brain mechanisms underlying this perception, and the striking lack of knowledge about the neuronal processing beyond the retina that might underlie that perception.

Possibly the largest group specifically interested in perception were psychologists who had accumulated a large number of observations about behaviour, many of whom were searching for an understanding of how the brain produced this behaviour. By the middle years of the 19th century, investigations in the laboratories of Fechner, Helmholtz and Wundt had established what became experimental psychology (for this history see Boring, 1950) so that by the 1950s a century of behavioural observations had accumulated. Studies on visual sensation and perception were prominent among them. Psychophysicists had studied visual perception by using controlled visual stimulation and precise measurements of behavioural judgements, and a wide range of visual phenomena had been studied including a plethora of intriguing visual illusions.

The Gestalt psychologists produced another line of visual experiments beginning in the early 20th century. Rather than concentrating on the elements of visual perception, they emphasized the wholeness of that perception. For example, the apparent motion between briefly flashed spots of light was based on the whole perception not the perception of the individual flashes. This was a very different approach to explaining visual perception, but it too led to interest in brain mechanisms, as illustrated below in an experiment by Kohler & Held (1949).

A second interest in neuronal mechanisms had been stimulated by the publication of *The Organization of Behaviour* in 1949 (Hebb, 1949). In this book Donald Hebb presented his ideas about brain organization underlying behaviour based not on logic diagrams but on the organization of neuronal circuits. His widely read ideas on cell assemblies and phase sequences, though based on hypothetical neurons, stimulated thinking about how neurons could be organized to produce complex behaviour. In Hebb's case this was largely directed at learning and memory, but it stimulated consideration of the neuronal mechanisms for visual perception as well.

The strength of interest in perception and the possible underlying brain mechanisms was matched by a paucity of physiological information, particularly at the neuronal level in cerebral cortex. Visual activity from cortex was usually recorded from the scalp of humans or the cortical surface of cats. The spatial representation of the visual

field in primary visual cortex, or striate cortex as it was usually referred to at the time, had been established in the cat and monkey by Talbot & Marshall (1941) who also noted the expansion of the size of the visual field representation between retina and cortex. G. H. Bishop had explored visual cortex but largely as an extension of determining the fibre distribution in the tracts projecting to cortex, and the origin of the evoked potentials within the cortex. (Bishop & Clare, 1955; Bishop & Clare, 1951; Bishop & Clare, 1952). He and Margaret Claire had, however, extended the region of cortex from which an evoked response could be obtained by identifying the first functionally defined extrastriate area, the Clare-Bishop area in the cat suprasylvian gyrus (Clare & Bishop, 1954). Richard Jung's laboratory had recorded single neurons in cat visual cortex but had concentrated on the excitatory and inhibitory responses of the half of the neurons they found that responded to diffuse light stimuli (Jung, 1958). Thus while there had been explorations of striate cortex, they produced little related to what it did. And this is what anyone interested in perception or visual behaviour wanted to know.

There were attempts to relate visual physiology to perception, but they were severely limited by the techniques available. An example of one of the best of these is an experiment by Wolfgang Kohler & Richard Held (1949) that I think illustrates both the interest in the neural mechanisms underlying perception and the severe limitations of the physiological techniques available. Kohler of course was one of the fathers of Gestalt psychology, which frequently invoked 'field' effects, and so it is not surprising that the experiment attempted to demonstrate the flow of current across visual cortex during pattern vision. Human subjects with an electrode over the presumed foveal representation in primary visual cortex fixated on a spot on a screen in front of them and a patterned stimulus was then passed across the fixation point. Kohler and Held found a voltage deflection as the pattern moved across the screen (Fig. 1). Their experiment shows in a snapshot the chasm existing between the motivation to understand the neural basis of perception and the methods most frequently used to study it. What is striking, however, is that key components subsequently used to study visual cortex by Hubel and Wiesel were in place: visual stimuli were presented to the subject while the eye did not move, and stimuli were not the diffuse flashes commonly used at the time. What was missing was the recording of an interpretable signal that could lead to understanding neuronal mechanisms; they recorded signals averaged over masses of neurons much like the EEG of that time or the fMRI of our time. Kohler and Held's concluding statement, however, was prophetic: 'In psychology, access to the cortical correlate of pattern vision would immediately affect the theory of psychophysical relations . . .'

It was against this background that the impact of Hubel and Wiesel's first paper (1959) can be appreciated. Their introduction set the tone: 'In the central nervous system the visual pathway from retina to striate cortex provides an opportunity to observe and compare single unit responses at several distinct levels. Patterns of light stimuli most effective in influencing units at one level may no longer be the most effective at the next. From differences in responses at successive stages in the pathway one may hope to gain some understanding of the part each stage plays in visual perception.' This introductory paragraph alone should have drawn the attention of any psychologist interested in the brain and any physiologist interested in the successive processing at higher and higher levels within the brain.

As indicated by their introduction, Hubel and Wiesel's experiments were not based on hypotheses about the mechanisms of perception or the neural activity already recorded from visual cortex, but rather on the previous observations on the ultimate input to the visual cortex, the retina. They built upon the elegantly precise work of their mentor Stephen Kuffler who had identified on- and off-centre ganglion cells in the cat retina and the centre and surround organization of these cells (Kuffler, 1953). More importantly they built on the Kuffler procedure of finding the stimulus required to activate each of the neurons encountered.

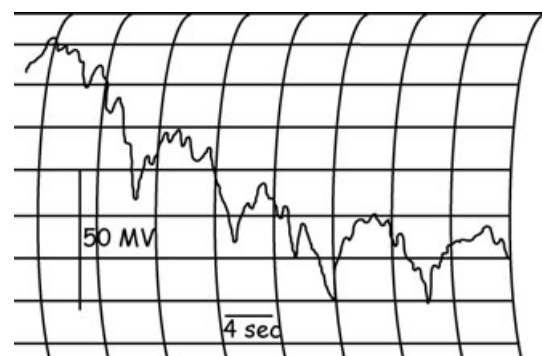
The central point of their initial finding in 1959 (Hubel & Wiesel, 1959) was that oriented slits of light were the most effective stimuli for activating striate cortex neurons in contrast to the spots of light Kuffler had found effective for ganglion cells. But the orientation selectivity resulted from the previous level of input because a neuron responding to a slit also responded to spots if they were aligned with the same orientation as the slit. Thus, in 10 figures they demonstrated the difference in the preferred stimulus for cortex compared to the retina how the cortical response could be derived from a lower level, and the possible contribution of excitatory and inhibitory regions of the circular receptive fields of the input neurons.

Hubel and Wiesel's experiments gave the first glimpse of how changes in the neuronal responses might lead to understanding the neuronal mechanisms underlying perception. For those interested in visual behaviour, it was also the first time they had real neuronal activity to stimulate their thinking about the possible organization of neurons for visual perception. Equally important, but less critical for those interested in behaviour, was the precise demonstration that the orientation processing was organized into columns of neurons within cortex, much as columns had been demonstrated previously in somatosensory cortex by Mountcastle (1957).

A second aspect of the initial experiments provoked even more interest: different neuron types in striate cortex could be viewed as steps in a hierarchy. The sequence from retina to cortex was evident in the 1959 paper, and in

their second paper (Hubel & Wiesel, 1962), they showed that within the striate cortex, a further level of processing could be identified between neurons referred to as simple cells and complex cells. Both types responded to oriented slits of light, but complex cells had a greater latitude in position of the slit and gave little response to spots of light. They argued that the properties of complex cells could more logically result from combining input from similarly oriented simple cells than from cells with circular receptive fields. These two steps were illustrated by simple logical connection diagrams (Hubel & Wiesel, 1962), which are reproduced in Fig. 2. The sequence from the retina to cortex and then within cortex illustrated how a sequence of neurons over a few synapses could represent stages of visual processing.

Hubel and Wiesel's findings were not just an advance but a quantum leap in our understanding of visual cortex. They showed how the pointillism of the retina is transformed into the orientation sensitivity in cortex. For those interested in the mechanisms of perception, their demonstration of successive transformations provided a glimpse of how perception might result from the organization of cortical neurons. At the physiological level, it led to thinking about the steps beyond striate cortex (which Hubel and Wiesel later explored 1965; 1969; 1970) and the nature of the transformations in these higher cortical areas (see for example Barlow, 1972). Thus, the experimental results and the hypotheses based on them began to fill the gap between the behaviourists search for mechanisms of visual perception and the neuronal activity that might provide such mechanisms. The search is far from over, but it was jump-started by the initial observations of Hubel and Wiesel.



**Figure 1. Response of human visual cortex to a moving visual pattern**

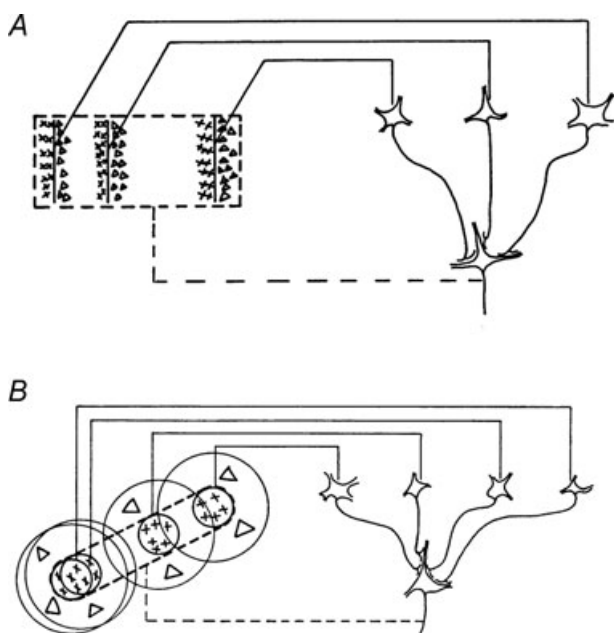
The figure was selected to illustrate the interest in seeing what brain activity underlies visual perception and the limited techniques available for studying that activity. In the experiment a 'bright moving object' was passed over the point of fixation. The figure shows the moving chart record of the activity evoked by four exposures of the object. Traced from Fig. 1 of Kohler & Held, 1949. Reprinted with permission from AAAS.

## Extending Hubel and Wiesel's findings to higher visual functions

All of Hubel and Wiesel's experiments were done on anaesthetized, paralysed animals, first on cats and then on monkeys. This provided the stability for single neuron recording and a stationary retina so that successive visual stimuli fell on the same region of the retina. Rapid or saccadic eye movements, which displace the retina several times per second in normal vision, were eliminated. But of course in normal vision these saccades as well as the small eye movements during fixation are always present. In addition, the normal cat or monkey is using the visual input to see the world and guide its behaviour.

One of the next steps in building on the discoveries of Hubel and Wiesel seemed to me to see how the visual system operated in the awake animal. To answer many of the questions on visual perception and the visual control of movement required an animal able to respond to the visual stimuli. But it was the framework Hubel and Wiesel had already provided for striate cortex that made the investigation of vision in the awake animal attractive.

The animal of choice to do these experiments was the old world monkey rather than the cat because of the monkey's ability to perform complex tasks and the similarity of its visual system to that of the human. I began trying to record



**Figure 2. Summary diagrams of the sequence of visual processing in striate cortex proposed by Hubel and Wiesel in 1962**

These two diagrams show the sequence proposed for the construction of the receptive types seen in cat striate cortex. *A*, the transformation from circular receptive fields to the elongated one of a simple cell. *B*, the construction of the receptive field of a complex cells from inputs from simple cells. From Hubel & Wiesel (1962).

from the striate cortex of awake monkeys in 1966, although at that time I was not certain that the old world monkey would be like the cat. My proximity to the laboratory of Edward V. Evarts at the NIH enabled me to use his tested techniques to record from awake monkeys, and to benefit from his generous help and advice. In first studying sleep and then the motor cortex of monkeys, Ed had worked out the technique for holding the head steady, and attaching a well-like base to the skull that permitted the introduction of a microelectrode through the dura into the cortex, and a microdrive that attached to the base and advanced the electrode. While Ed was not the first to record from awake monkeys (see Jasper *et al.* 1958), he had developed an integrated system of head restraint and recording (Evarts, 1966, 1968). His microdrive and implanted base were modifications of that designed by David Hubel who had himself recorded from the lateral geniculate and striate cortex in the awake cat free to move its eyes (Hubel, 1959, 1960). Hubel's finding that many neurons that did not respond to diffuse light stimuli did respond to small spots (Hubel, 1959) was overshadowed by the report of their systematic recordings in the anaesthetized cat appearing in the same year (Hubel & Wiesel, 1959).

The remaining problem with the awake monkey, however, was eye movements. Without going into details, that turned out to be soluble; the monkeys were trained to fixate on a target and detect its dimming. With this technique, the monkeys were rewarded for fixating for several seconds and I was rewarded by having several seconds in which I could search for a neuron's receptive field with a spot or slit of light turned on just during the fixation. After the reward the monkey would break fixation, the receptive field would move with the eye, but by that time the stimulus had been turned off. The whole procedure began again during the next fixation. The method for the awake monkey behaviour was basically the same as that used by Albert Fuchs in David Robinson's laboratory at Johns Hopkins (Fuchs, 1967) except that he was rewarding the monkey to make eye movements and I was rewarding it not to make them.

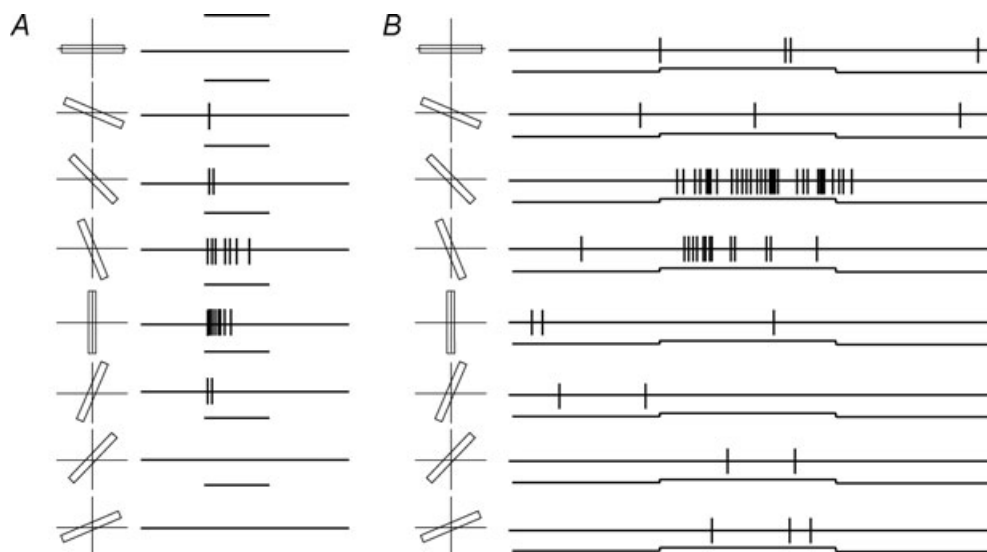
I wanted to make the experimental conditions roughly comparable to those of Hubel and Wiesel so that I could show clearly the many differences I expected to find in the awake compared to the anaesthetized animal. This was largely possible because of David Hubel's invitation several years earlier to watch one of their experiments. That visit to their lab was both the source of the essential understanding of how they went about mapping and characterizing a striate cortex neuron's receptive field and the source of inspiration to do it in the awake animal. Torsten Wiesel also made a brief visit to my laboratory at the NIH during the early experiments, and I was both encouraged by his interest and relieved that he did not point out some fatal flaw in what I was doing.



My initial explorations showed that in the awake monkey with normal eye motion during visual fixation it was readily possible to identify neurons that responded best to oriented stimuli, that cells with simple receptive fields could be distinguished from those with complex receptive fields, and that simple receptive fields could be mapped with spots of light (Wurtz, 1969c). Figure 3 shows side by side a simple cell from Hubel and Wiesel's 1959 cat paper and from my 1969 monkey paper. My example neuron was obviously selected as one that clearly showed the orientation selectivity previously found in the cat. There were also directionally selective motion cells as well as cells that did not require oriented stimuli, both findings that were in Hubel and Wiesel's 1968 paper on the old world monkey striate cortex.

The good news was that the basic observations in the awake monkey were comparable to those Hubel and Wiesel found first in the anaesthetized paralysed cat (Hubel & Wiesel, 1959, 1962) and later in the monkey (Hubel & Wiesel, 1968). What my experiments showed was that the orderly visual transformations were not some anaesthesia induced perturbation of normal visual processing. Of course I was relieved to see this; I certainly would not have gone to all the effort to develop the method had I thought all that order would disappear in the awake animal. Furthermore the addition of the small eye movements presumably present during fixation also did not disrupt the mapping of visual receptive fields, and this opened the way for investigating the organization and modulation of visual response in both striate cortex and areas beyond it.

The bad news, at least in my view, was that I found little that was new in the awake monkey, at least not at the qualitative level I was investigating. I thought it likely that a corollary discharge postulated by Sperry (1950) and von Holst and Mittelstaedt (1950) might be evident in striate cortex. Such an input would solve the problem of the disruptive sweep of the visual world with each saccade because input to striate cortex from a corollary of the saccade could reduce neuronal activity resulting from the saccade, possibly even producing the 'central anaesthesia' postulated by Holt (1903). It made sense to remove the disruption in the striate cortex neurons because then the disruption would be removed for all higher levels of processing. It was not removed (Wurtz, 1969a,b). I also thought that neurons in the awake monkey might be essentially gated by visual attention and they were not (Wurtz & Mohler, 1976). We now know that many of the modulations I thought I would find in striate cortex are indeed found in cortex, but they become prominent after visual information reaches higher levels. Modulation with saccades is not clearly evident until the middle temporal area (for a review see Wurtz, 2008). The corollary discharge itself has only recently been identified, not in occipital cortex, but in the pathway to frontal cortex (Sommer & Wurtz, 2006, 2008). Attention has been identified in striate cortex (Posner & Gilbert, 1999), and even in the lateral geniculate nucleus (McAlonan *et al.* 2008), but the modulation is only about 10%. In extrastriate areas it rises to at least 40% (Maunsell & Cook, 2002). I think the first new observation in striate cortex found in awake monkeys



**Figure 3. Example simple cells in the striate cortex of anaesthetized paralysed cat (A) and the awake fixating monkey (B)**

The comparison illustrates the similar response to oriented slits of light in the anaesthetized, paralysed cats and awake behaving monkeys. The example from the awake monkey shows the same qualitative orientation tuning but a slightly higher background rate than from the anaesthetized cat. Traced from Fig. 3A of Hubel & Wiesel (1959) and from Fig. 5 of (Wurtz, 1969c).

was the later demonstration of disparity sensitivity (Poggio *et al.* 1977; Poggio & Talbot, 1981).

This expectation of being able to relate neuronal activity to higher levels of visual processing has been realized not so much in striate cortex, but in the substantial series of functionally specific areas carved out of what was loosely referred to as areas 18 and 19 (Zeki, 1978; Felleman & Van Essen, 1991). Explorations of these areas has relied on the use of awake monkeys that enables both the comparison of changes in behavioural report with changes in neuronal activity and alteration in these reports when the neurons are perturbed by stimulation or inactivation. These methods have enabled the investigation of the neuronal activity underlying visual perception, cognitive behaviour, and the control of movement that have flourished in the last 25 years. It is, however, Hubel and Wiesel's work starting in 1959 that remains the basis of these subsequent investigations and I think a major source of inspiration to do them.

## References

- Barlow HB (1972). Single units and sensation: a neuron doctrine for perceptual psychology? *Perception* **1**, 371–394.
- Bishop GH & Clare M (1951). Radiation path from geniculate to optic cortex in cat. *J Neurophysiol* **14**, 496–505.
- Bishop GH & Clare MH (1952). Sites of origin of electric potentials in striate cortex. *J Neurophysiol* **15**, 201–220.
- Bishop GH & Clare MH (1955). Organization and distribution of fibers in the optic tract of the cat. *J Comp Neurol* **103**, 269–304.
- Boring EG (1950). *A History of Experimental Psychology*. Appleton-Century-Crofts, New York.
- Clare MH & Bishop GH (1954). Responses from an association area secondarily activated from optic cortex. *J Neurophysiol* **17**, 271–277.
- Evarts EV (ed) (1966). *Methods for Recording Activity of Individual Neurons in Moving Animals*, vol. 2. Year Book, Chicago.
- Evarts EV (1968). A technique for recording activity of subcortical neurons in moving animals. *Electroencephalogr Clin Neurophysiol* **24**, 83–86.
- Felleman DJ & Van Essen DC (1991). Distributed hierarchical processing in the primate cerebral cortex. *Cereb Cortex* **1**, 1–47.
- Fuchs AF (1967). Saccadic and smooth pursuit eye movements in the monkey. *J Physiol* **191**, 609–631.
- Hebb DO (1949). *The Organization of Behavior*. A Neuropsychological Theory. John Wiley & Sons, New York.
- von Holst E & Mittelstaedt H (1950). Das reafferenzprinzip. Wechselwirkungen zwischen zentralnervensystem und peripherie. *Naturwissenschaften* **37**, 464–476.
- Holt EB (1903). Eye-movement and central anaesthesia. I. The problem of anaesthesia during eye-movement. *Psychol Monogr* **4**, 3–46.
- Hubel DH (1959). Single unit activity in striate cortex of unrestrained cats. *J Physiol* **147**, 226–238.
- Hubel DH (1960). Single unit activity in lateral geniculate body and optic tract of unrestrained cats. *J Physiol* **150**, 91–104.
- Hubel DH (1982). Cortical neurobiology: a slanted historical perspective. *Annu Rev Neurosci* **5**, 363–370.
- Hubel DH & Wiesel TN (1959). Receptive fields of single neurones in the cat's striate cortex. *J Physiol* **148**, 574–591.
- Hubel DH & Wiesel TN (1962). Receptive fields, binocular interaction and functional architecture in the cat's visual cortex. *J Physiol* **160**, 106–154.
- Hubel DH & Wiesel TN (1965). Receptive fields and functional architecture in two nonstriate visual areas (18 and 19) of the cat. *J Neurophysiol* **28**, 229–289.
- Hubel DH & Wiesel TN (1968). Receptive fields and functional architecture of monkey striate cortex. *J Physiol* **195**, 215–243.
- Hubel DH & Wiesel TN (1969). Visual area of the lateral suprasylvian gyrus (Clare-Bishop area) of the cat. *J Physiol* **202**, 251–260.
- Hubel DH & Wiesel TN (1970). Stereoscopic vision in macaque monkey. Cells sensitive to binocular depth in area 18 of the macaque monkey cortex. *Nature* **225**, 41–42.
- Hubel DH & Wiesel TN (2005). *Brain and Visual Perception. The Story of a 25-Year Collaboration*. Oxford University Press, Oxford.
- Jasper H, Ricci G & Doane B (1958). Patterns of cortical neuronal discharge during conditioned response in monkeys. In *Ciba Foundation Symposium on the Neurological Basis of Behavior*. Little Brown, New York.
- Jung R (1958). Excitation, inhibition and coordination of cortical neurones. *Exp Cell Res* **14**, 262–271.
- Kohler W & Held R (1949). The cortical correlate of pattern vision. *Science* **110**, 414–419.
- Kuffler SW (1953). Discharge patterns and functional organization of mammalian retina. *J Neurophysiol* **16**, 37–68.
- Maunsell JH & Cook EP (2002). The role of attention in visual processing. *Philos Trans R Soc Lond B Biol Sci* **357**, 1063–1072.
- McAlonan K, Cavanaugh J & Wurtz RH (2008). Guarding the gateway to cortex with attention in visual thalamus. *Nature* **456**, 391–394.
- Mountcastle VB (1957). Modality and topographic properties of single neurons of cat's somatic sensory cortex. *J Neurophysiol* **20**, 408–434.
- Poggio GF, Doty RW Jr & Talbot WH (1977). Foveal striate cortex of behaving monkey: single-neuron responses to square-wave gratings during fixation of gaze. *J Neurophysiol* **40**, 1369–1391.
- Poggio GF & Talbot WH (1981). Mechanisms of static and dynamic stereopsis in foveal cortex of the rhesus monkey. *J Physiol* **315**, 469–492.
- Posner MI & Gilbert CD (1999). Attention and primary visual cortex. *Proc Natl Acad Sci U S A* **96**, 2585–2587.
- Sommer MA & Wurtz RH (2006). Influence of the thalamus on spatial visual processing in frontal cortex. *Nature* **444**, 374–377.
- Sommer MA & Wurtz RH (2008). Brain circuits for the internal monitoring of movements. *Annu Rev Neuroscience* **31**, 317–338.
- Sperry RW (1950). Neural basis of the spontaneous optokinetic response produced by visual inversion. *J Comp Physiol Psychol* **43**, 482–489.

- Talbot SA & Marshall WH (1941). Physiological studies on neural mechanisms of visual localization and discrimination. *Am J Ophthalmol*, 1255–1263.
- Wurtz RH (1969a). Comparison of effects of eye movements and stimulus movements on striate cortex neurons of the monkey. *J Neurophysiol* **32**, 987–994.
- Wurtz RH (1969b). Response of striate cortex neurons during rapid eye movements in the monkey. *J Neurophysiol* **32**, 975–986.
- Wurtz RH (1969c). Visual receptive fields of striate cortex neurons in awake monkeys. *J Neurophysiol* **32**, 727–742.
- Wurtz RH (2008). Neuronal mechanisms of visual stability. *Vision Res* **48**, 2070–2089.
- Wurtz RH & Mohler CW (1976). Enhancement of visual responses in monkey striate cortex and frontal eye fields. *J Neurophysiol* **39**, 766–772.
- Zeki SM (1978). Functional specialisation in the visual cortex of the rhesus monkey. *Nature* **274**, 423–428.

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