Neuronal mechanisms for the perception of ambiguous stimuli
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Ambiguous figures that may take on the appearance of two or more distinct forms have fascinated philosophers and psychologists for generations. Recently, several laboratories have studied the neuronal basis of perceptual appearance at the level of single neurons in the cerebral cortex. Experiments that integrate neuronal recording with analyses based on sensory detection theory reveal a remarkable degree of specificity in these neuronal responses. The new challenges are to understand how cognitive processes, such as attention and memory, interact with perception to generate these neuronal signals.

Introduction
‘I contemplate a face, and then suddenly notice its likeness to another. I see that it has not changed; and yet I see it differently. (The) causes are of interest to psychologists.’

Ludwig Wittgenstein Philosophical Investigations [1].

Many figures change in a discrete and salient way during viewing. The quotation highlights the experience of suddenly appreciating the resemblance of one figure to another. When this happens, the figure that we are viewing does not change materially, yet the significance of features in the figure is altered by our cognitive processes.

The most intriguing figures of this type are perceptually ambiguous. Such figures provide the experience of looking at a constant external stimulus whose perceptual appearance changes from one viewing to the next, or indeed from one moment to the next in continuous viewing. Figures of this type have fascinated philosophers and psychologists for generations because they offer insight into the cognitive, mental processes of perception. Neuroscientists have the same motivation as earlier scholars. Examples of current interest are found in binocular rivalry [2,3*], perception of three-dimensional shapes [4–7], motion perception [8] and figure–ground relationships [9,10].

The study of how the brain responds to a shift in the perceptual appearance of a figure provides insights into neuronal processes that are crucially associated with perceptual decision-making. In the ideal case, the neuronal signals do indeed reflect the shift in perceptual appearance, because the external stimulus delivered to the sensory receptors remains the same. Thus, (it is argued) these particular neuronal signals reflect a form of mental processing that is ‘higher’ or ‘deeper’ than simple detection and analysis of the external sensory stimulus. Such processing may reflect the influence of experience in the form of memory and cognition. More speculatively, the neuronal signals could reflect conscious perception or even an ‘act of will’ in taking up one perceptual interpretation rather than another. Such interpretations would elevate the neuronal signals under study to ‘neuronal correlates of consciousness’ [11–14].

Exciting although such interpretations may be, there are numerous obstacles in the way of moving forward with this programme of work. Nonetheless, we argue here that the past few years have seen some striking advances in the identification of neuronal signals related to perception. Improved knowledge about the sources and sites of these signals has come from the steady application of single-unit recording and, more recently, the use of new technologies (functional magnetic resonance imaging [fMRI], magneto-encephalography and other brain imaging). The development of novel behavioural paradigms (particularly for application with non-human subjects) has enabled a new range of studies at the level of single neurons. In conjunction with these advances, it has been proposed that one might be able to use perceptual paradigms, such as multistable figures, as a psychobiological probe of cognitive traits associated with affective or other mood disorders in humans [15].

The simple identification of a physiological signal as a putative ‘neuronal correlate of perception’ is less novel and newsworthy as a research result than it once was. Significantly, our understanding of perceptually relevant signals has developed considerably with new theoretical approaches. Psychophysical and neurophysiological studies that employ rigorous statistical methods for analysing performance in making sensory decisions [16] provide powerful results that are now being used in the study of perceptual ambiguity. This is exerting a drive towards finding answers that provide a quantitative account of...
firing patterns within populations of cortical neurons. Second, investigators are now beginning to think about the relationships among the particular signals that correlate with perceptual decisions when subjects view ambiguous figures and the more general neuronal signals that are involved in perceptual and cognitive decisions. For example, neuronal mechanisms that underlie attention have been studied in depth in the past few years [17–19], and an important future activity is to determine how the signals identified in the attention paradigm relate to those identified in perceptual decision-making [20].

As the focus here is on sensory decision-making, positive emphasis in selecting papers for discussion has been given to experiments that measure signals at the level of single neurons and small neuronal populations rather than at the level of cortical areas or regions. Consequently, we feature most strongly the responses of neurons in non-human primates that have been trained to make perceptual judgments about perceptually ambiguous stimuli. The extensive literature that uses the technique of human brain imaging is discussed mainly as a source for correlative information.

**Multistable figures**

There are many examples of multistable figures. Normally, these figures may be seen in one of two different configurations, although some have more than two possibilities. At any one time, the configuration that is dominant excludes or suppresses the perception of the alternative configurations. The quotation at the beginning reminds us that this experience of perceiving distinct configurations is not unique to multistable figures. What is particularly characteristic about multistable figures is that the different configurations possess roughly equal saliency or power to dominate perception.

True rivalry, as in binocular rivalry, involves something that is physically present but not perceived (the suppressed stimulus). In contrast, in a figure such as the Necker cube (Figure 1) or the cylinder paradigm that we discuss in detail later (Figure 2), the entire stimulus configuration is consumed by one perceptual interpretation, leaving nothing residual the perception of which is suppressed. Neuronal responses to suppressed stimuli have been studied with a specific paradigm of flash suppression as well as with binocular rivalry. In both paradigms, suppressed stimuli provide one index of whether or not neuronal firing is directly linked with conscious perception of objects. If neurons continue to fire to suppressed stimuli, then it is argued that they cannot be directly involved in conscious perception [21,22]. Indeed, some neurons are reported as becoming more active when their preferred stimulus (as assessed with unambiguous stimuli) is suppressed [2,23].

With figures such as the Necker cube, the two interpretations form distinct complementary categories and the instability lies at the boundary of these categories. As in the binocular rivalry paradigm, it is natural to interpret...
the instability as the alternating dominance of one of a pair of neuronal populations. Specifying the nature of the neuronal signals that reflect this dominance is a goal of current research. We would like to know the location, size and composition of the two hypothesized neuronal populations, the identity of the signals that are present during dominant and non-dominant phases, the way that those signals are distributed within the population and whether or not there is a unique neuronal signature associated with the moment of switching from one perceptual interpretation to another.

These questions are currently approached with two main types of paradigm. In continuous viewing, the ideal situation is to obtain a lengthy period during which the subject views a multistable figure and reports which percept dominates at any one time. Simultaneous neuronal recordings are made so that the temporal correlation of neuronal and perceptual changes can be assessed. In the other paradigm, a multistable figure is presented for a single fixed duration (much shorter than the average switching time in continuous viewing) and the subject is required to choose one of two alternatives to make a perceptual report at the end of the trial. Again, a correlation of neuronal activity and perceptual decision is the measured outcome.

**Precision of neuronal correlates of perception**

Although this account is straightforward, real applications of these paradigms are considerably more complex. Most of the reasons for this complexity arise from the fact that these measures are simply correlations. Unless several rigorous controls are conducted, there is always the danger that the underlying cause of the correlations measured in a particular neuronal population may actually arise from the activity of a third neuronal population in which activity has not been monitored. This third population might not even be connected anatomically with the neurons from which recordings have been made. For example, if a subject makes a characteristic eye movement in association with a particular perceptual decision, then that eye movement may generate changes in the retinal image that affect populations of visual neurons that are unrelated to the perceptual decisions. Although changes of this type are often classed as spurious, it should be recognized that they must inevitably form a component of the brain’s responses during natural viewing, such as looking informally at multistable figures.

A complementary issue regarding correlation measures is that they can easily be diluted by measurement error. For example, if the subject does not report the percepts honestly, these inaccuracies will dilute correlations that ought to have been revealed. This problem is most acute when working with non-human primates whose behav-

ional strategy is to exploit the experimental paradigm to maximise the delivery of rewards. However, human observers are not immune from these lapses, particularly during the long periods of observation that are needed either to characterize some types of perceptual switch or to collect the slow haemodynamic responses in fMRI experiments. The main approach to combat these lapses is to include ‘catch trials’, in which unambiguous stimuli are presented so that the honesty of the observer can be evaluated. For this approach to be completely effective, there should be no perceptual difference between an ambiguous stimulus that is currently engendering one perceptual state and the unambiguous stimulus that corresponds to that perceptual state.

A related issue is raised by the use of behavioural measures that substitute for perceptual reports. For example, the way in which the eyes follow the movement of individual components of a pair of binocularly rivalrous patterns is strongly linked to whichever pattern is perceptually dominant at any one time. This means that optokinetic responses can be used as an ersatz index of perceptual dominance without the need to train animals to respond behaviourally [24–26]. Although the correlation between perceptual reports and eye movements is high, it is not perfect [24], for reasons that are not wholly clear. It should not be automatically assumed that the perceptual reports are perfect and that the problem lies with the substitute measure that is formed on the basis of eye movements. Whatever the case, this is another factor that can dilute correlations between neuronal signals and perceptual dominance.

**Sites of perceptual decision-making**

At the neuronal level, the continuous viewing paradigm has largely been used in connection with binocular rivalry or the related paradigm of flash suppression [2,3,7,11,22,27]. The emerging view is that the neuronal correlates of binocular rivalry are widely dispersed throughout many areas of the visual cortex and beyond. A similar observation has been made for rivalrous motion stimuli [28].

On the one hand, this observation is arguably unsurprising from the viewpoint that the relevant neuronal site that causes the change in percept is early in the visual pathways: all sites deeper in the pathway will reflect the modulation by these earlier neurons. On the other hand, it is also possible to sustain an argument that the causally relevant site(s) for rivalry may be deep in the pathways: according to this view, the modulation seen in earlier areas is a correlate of the activation derived from sites deep in the cortex that send feedback to earlier sites. Finally, there is a third perspective on rivalry that attempts to take a middle way: here it is argued that the competitive nature of interactions among neuronal populations is played out simultaneously at multiple levels within the nervous system. In all three cases,
the argument can be made that sites showing signs of perceptual modulation ought to be dispersed throughout wide regions of the visual brain.

Some ways of breaking this deadlock are therefore required. In the case of binocular rivalry, interest has centred on the question of whether or not the rivalry is truly eye-related (early) or percept-related (late) [3*,27, 29,30,31*]. It is increasingly clear that both forms of rivalry may be predominant under different conditions. In one recent example, Bonneh et al. [32*] used composite stimuli with Gabor patches of aligned or random orientations. (A Gabor patch is a small oriented feature whose spatial luminance profile is formed by the multiplication of a sinusoidal waveform with a Gaussian envelope.) Orientation jitter breaks up any pattern, therefore favouring eye-rivalry rather than percept-rivalry. There is a gradual shift from eye-rivalry to percept-rivalry as pattern coherence is increased, thus a reconciliation of apparently conflicting results is offered.

Several avenues now need to be pursued. First, the timing relationships among the perceptually related signals that are found in different cortical areas need to be explored. Relevant neuronal activity often occurs in advance of the perceptual report by up to 1 s [2], but the greatest precedence should clearly be accorded to sites with the earliest activity. This will require recordings to be made simultaneously from multiple neurons within identified brain areas and from multiple brain areas. Some recent studies highlight the potential complexity of events when switches occur in binocular rivalry. Wilson et al. [33] placed a conventional binocular rivalry stimulus in the spatial form of a thin-ringed annulus. They observed that the switch of visibility from one stimulus to the other propagated systematically around the annulus. They were able to estimate the speed of propagation, and proposed that this might reflect the dynamics of a physiological process that travels across the cortical surface. The neuronal correlates of such a process would inevitably have a complex time structure. A parallel issue has also been reported in the featural domain [34], in which a disjunction between the rivalry of orientation and motion direction has been observed (see also [35]). Thus, neurons selective for orientation but not selective for motion direction might have a time-course of activations that reflect the perceptual rivalry attached to orientation, whereas neurons selective for direction of motion might have a different time-course that reflects the temporal sequence of perceptual changes in motion direction.

Second, sites in which sensory evidence and decision-related activity converge also need detailed examination. In normal situations, perceptual decisions are based on a combination of prior knowledge and evidence about the current state of the world. Brain sites that actually play a central role in perceptual decisions should show signs of integrating these two types of signal. Specifically, in considering ambiguous stimuli, the most interesting brain sites are those that represent both alternatives but have a preponderance of activity in favour of the perceptual decision when the ambiguous stimulus is presented. Sites that represent only the perceptual decision to the complete exclusion of the alternative would presumably be post-decision, whereas sites that reflect only the external stimulus with no decision-related activity are also of little explanatory value.

Third, and most crucially, there need to be attempts to intervene causally in the decision-making process. Unfortunately, the range of techniques that are of value here is limited. Ideally an intervention should act in some specific way, such as shifting the pattern of perceptual reports in favour of one alternative without otherwise disrupting perceptual performance or specifically changing the rate of alternation [15]. The most promising approach is electrical microstimulation, which has been used successfully to intervene in the formation of sensory decisions by the application of focal activation to small groups of neurons and their connections [36,37]. Another possibility would be the brief and reversible application of pharmacological agents.

**Forcing a decision**

A different approach to monitoring responses to perceptually ambiguous stimuli is to make stimulus presentations of fixed duration that require a decision at the end of the presentation. The duration must be short, so that there is a very small chance of instability during the single presentation. Although there is then no chance of examining the neuronal responses to perceptual switches, there are several compensating advantages, which are illustrated by the use of ambiguous structure-from-motion stimuli [4,5,38,39,40*,41].

These stimuli depict rotating spheres or cylinders by means of a pattern of random dots in motion (see Figure 2). The dots are arranged on two transparent superimposed surfaces and the movement of the dots is consistent with a global rotation of the figure. The ambiguity of these figures lies in the fact that any particular pattern of dot movements is by itself consistent with either one or the other of the two possible directions of rotation. A set of dots that is moving rightwards on a vertically oriented cylinder rotating about its principal axis is consistent with a clockwise rotation of the cylinder if the dots are on the rear surface but a counter-clockwise rotation if the dots are on the front surface. The ambiguity can be resolved by adding binocular stereoscopic disparity to the display. Front and rear can then be defined by separating the rightward and leftward moving dots in binocular depth so that the direction of rotation is fixed.
The main advantage is that it becomes much easier to embed ambiguous stimuli as relatively rare events within a sequence of trials that are mostly unambiguous. As the behavioural response on unambiguous trials is always right or wrong, this provides a way of probing the honesty of the subject’s responses. Indeed, if the set of unambiguous stimuli is placed in the range of the sensory detection threshold for stereo disparity [40*], it becomes impossible to distinguish unambiguous from ambiguous stimuli. The only way for the subject to maximise the proportion of correct responses is to treat all stimuli as unambiguous and respond accordingly. An important observation is that the switching times during continuous viewing are much longer than the one or two second trials used for fixed-duration presentations (E. Brunskill, et al. unpublished data).

Under these conditions, neurons in the extrastriate cortical area V5/MT exhibit a remarkable degree of specificity in signalling the reported percept with ambiguous stimuli. V5/MT neurons that show a sensory preference for clockwise rotation of unambiguous stimuli also show enhanced firing in response to ambiguous stimuli when they are reported as having clockwise rotation. This enhancement of firing represents a tight correlation between neuron and behaviour, as is shown by the high values of choice probability in this task [40*]. Listening to the output of just the average neuron in this brain area during a single trial gives a chance better than 2:1 of correctly predicting the perceptual choice at the end of the trial, with some individual neurons showing much higher reliability.

An important aspect of these recent data is the absence of neurons that show a sensory preference for one direction of rotation and a decision-related response to the opposite direction of rotation. This result differs from earlier measurements of single-neuron correlates of perception [2,5,23,41]. There may be two reasons for this. First, in the binocular rivalry paradigm the perceptually suppressed stimulus is still physically present on the retina and some neurons respond to it. For the cylinder paradigm, every physically present dot is always accounted for by the current perceptual interpretation, with no dots left over. Second, the monkeys in the study by Dodd et al. [40*] were specifically required to work at a psychophysical threshold, which may effect a tighter link between decision-related firing and behavioural choice, perhaps through a tighter control of attention.

Decision-making about the perceptual appearance of the ambiguous stimulus is tightly coupled to the activity in two sensory pools of neurons. One pool favours clockwise rotation and the other counter-clockwise rotation. There are two competing hypotheses for enhanced firing in the currently favoured pool. According to one hypothesis, the fluctuations of firing in sensory signals within V5/MT are sufficient to flip perception one way or another. This event could then be reinforced by a feedback signal that is generated internally within V5/MT and stabilizes the current perceptual interpretation. With the other hypothesis, the enhanced firing observed in V5/MT reflects a perceptually related signal that is derived from higher-order cortical areas. Both ideas are consistent with the greater size of choice probabilities for ambiguous cylinders [40*] when compared with random motion [42].

Current thinking places this decision-making process close to the one that is hypothesized to underlie the sensory discrimination of motion direction [16,42,43] and binocular disparity [44] in the same cortical area. However, there are some marked differences. Importantly so far, no positive effect of electrical microstimulation [36,44] on the perception of ambiguous structure-from-motion stimuli has been identified. In addition, in the motion and disparity studies, the neutral stimulus is a field of dots with a noisy structure, which is qualitatively different from fields of dots that are all moving in the same direction (in the motion study) or all at the same depth plane (in the disparity study). This contrasts sharply with the two distinct perceptual interpretations for the ambiguous rotating cylinder. The neutral motion stimulus itself contains random fluctuations that could potentially favour a particular motion direction, although these fluctuations are not responsible for driving the correlation of behavioural decision and neuronal activity in the detection of motion [42]. For the ambiguous cylinder, a momentary excess of rightward moving dots does not inherently favour the perception of either clockwise or counterclockwise rotation.

**Conclusions**

Our best indications are that the resolution of perceptual ambiguity proceeds at the neuronal level in much the same way that other perceptual decisions are formed [45**]. The activity of pools of sensory neurons contributes evidence over a time period of decision formation. This period may be terminated either spontaneously or by the removal of the stimulus. Alternatively, during prolonged viewing, the time-period slides continuously such that the most recent evidence receives the strongest weighting. The neuronal characteristics that favour perceptual ambiguity within a stimulus are that the activity levels of two competing pools of sensory neurons are closely balanced and that the pools represent two, highly distinct perceptual categories. Even small changes in the sensory evidence – changes near the psychophysical threshold – can favour one perceptual state over the other. Within V5/MT, the correlation of neuronal responses with perceptual choice is numerically larger in the case of ambiguous stimuli [40*] than it is during discrimination of motion direction [42]. By itself, this might suggest that decision-related activity with ambiguous stimuli is more tightly focussed within a smaller group of
neurons. Such an interpretation cannot be rejected for now. However, a serious alternative hypothesis is that decision-related activity may reflect the neuronal correlates of other cognitive processes, such as attention, as well as the formation of the decision itself [20,46]. Future experiments will need to make overt manipulations of attentional processes to evaluate this issue.

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References and recommended reading

Papers of particular interest, published within the annual period of review, have been highlighted as:

• of special interest

**of outstanding interest


An invaluable summary that is written chiefly from the perspective of rivalrous percepts.


The authors present a study that exploits the rare possibility of recording directly from single cortical neurons in conscious human subjects.


An ingenious study that exploits the monococular representation of the blind-spot in the primary visual cortex to study the fMRI signals associated with a switch in visibility in binocular rivalry.


This study makes a test of the hypothesis about pattern rivalry by specifically manipulating the coherence of oriented regions in the rivalrous patterns.


  The authors find that during perceptual judgments about ambiguous figures, V5/MT contains decision signals that are statistically strong and, importantly, specific to the way that the neuron responds to unambiguous figures.


  The authors present a synthesis of recent advances in understanding how neuronal pools contribute to the formation of perceptual decisions.


47. Wheatstone C: Contributions to the physiology of vision: II. On some remarkable, and hitherto unobserved, phenomena of binocular vision (continued). *Philos Trans R Soc Lond* 1852, 142:1-17.