Neuronal activity and its links with the perception of multi-stable figures

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In order to isolate the neuronal activity that relates to the making of perceptual decisions, we have made use of a perceptually ambiguous motion stimulus. This stimulus lies on the boundary between two perceptual categories that correspond to clockwise and counter-clockwise rotation of a three-dimensional figure. It consists of a two-dimensional pattern of moving dots that are capable of generating these two, distinct, three-dimensional percepts. We have studied the responses of neurons in cortical area V5/MT whilst macaque monkeys report judgements about the perceptual configuration of this stimulus. We extract a quantitative statistic called 'choice probability' that expresses the covariation of neuronal activity and perceptual choice. An analysis of choice probabilities shows that the pool of neurons involved in the perceptual decisions is a tightly constrained subset of the population of sensory neurons relevant to the perceptual task.

Keywords: perceptual decision; extrastriate cortex; vision

1. INTRODUCTION

Since the 19th century, the search for localization of function within the brain has become steadily more intense. The fundamental significance of many regions of the cortex has been recognized, such that we are now able to identify with certainty, in a given individual, that some cortical regions are always associated with specific aspects of motor function, others with specific topographical maps of visual information, and so on. This understanding has been achieved through a multi-disciplinary approach, involving the integration of information from studies of humans who have suffered accidental brain damage, and studies of animals in which discrete lesions have been placed experimentally.

In parallel, the anatomical study of the cellular structure of the nervous system has identified the single neuron as the elementary building block from which the operations of the nervous system are constructed. Although it is now very clear that single neurons have a fundamental role in the cellular organization and signalling of the cortex, it remains unclear whether analysis at the level of single neurons provides a sufficient basis for understanding the functional operations of the nervous system. Of particular interest are the means by which it supports important cognitive functions, such as perception, attention, learning, memory and the planning and execution of movements.

Barlow (1995) has cogently argued that the signals within single nerve cells are central to understanding the operation of the nervous system. In his view, the firing of individual nerve cells amounts to a form of assertion about the presence of stimulus features in the environment. In his original conception, Barlow (1972) considered perceptual decisions to be governed, not uniquely by a single neuron, but by a small number of highly influential neurons: Barlow specifically used the analogy of a 'College of Cardinals', who 'directly and simply cause the elements of our perception'.

2. NEURONAL ACTIVITY AND MULTI-STABLE FIGURES

From this perspective, experimental investigations of a relationship between the firing of single neurons and perceptual decisions are of great significance. Nonetheless, several serious issues arise, if one simply approaches this question by choosing a set of stimuli and proceeding to explore the firing patterns of sensory neurons. First, unless a psychophysical observer is set a particular task to perform, there is no guarantee that any perceptual decision is formed. Furthermore, in order to ensure the accuracy of these perceptual decisions, it is necessary to monitor the level of performance of the task. Second, when sensory neurons are excited by a range of external stimuli, changes in the firing patterns of those neurons may arise for two distinct reasons. One source of excitation arises from factors that are genuinely related to the perceptual decisions made by the observer. These are the factors that we wish to isolate and study. The other source of excitation is more commonly studied and in many ways better understood: for any neuron that is tuned to a sensory stimulus, much of the change in firing rates will simply reflect the fact that some stimuli are more effective than others in exciting the neuron.

For this reason, an ideal configuration for studying, in isolation, the factors that lead to perceptual decisions is one in which the external stimulus is constant but its perceptual interpretation may change. The classic examples

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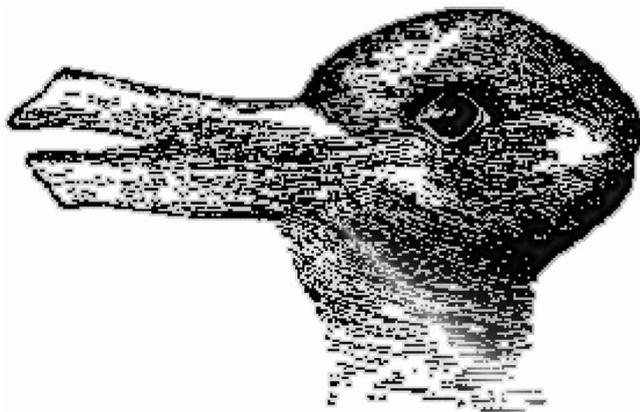
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Figure 1. This perceptually reversible figure was devised in 1900 by the psychologist Jastrow and is universally referred to as the 'duck–rabbit' figure.

of this type are given by perceptually ambiguous figures, such as the duck–rabbit figure devised by Jastrow (see figure 1). In this case, the figure may be seen either as the drawing of a duck or as the drawing of a rabbit. Another example is the Necker cube, in which a picture of a wire-frame cube can take on one of two interpretations as a perspective representation of the cube.

Clearly, in order to exploit ambiguous figures of this kind in a neurophysiological experiment, it is necessary to make reliable recordings from neurons that respond selectively to one of the unambiguous versions of these figures. Neurons of this type are found mostly at high levels of visual processing within brain areas, such as the infero-temporal cortex. Selectivity for these parameters entails the presence of signals relating to object identity (in the case of the duck–rabbit) or three-dimensional linear perspective (in the case of the Necker cube). The diversity of possible selectivity for visual features, and the fact that such neurons are widely dispersed anatomically, makes this experimental approach difficult. Accordingly, simpler paradigms have been sought that rely upon features of visual coding that are more commonly encountered at earlier stages within the visual pathway.

(a) *Binocular rivalry*

One example is presented by binocular rivalry, in which dissimilar patterns, such as horizontal and vertical stripes, are presented to the left and right eyes of an observer. Under these conditions, the patterns do not fuse into a single binocular object but the visibility of the patterns alternates. This change in appearance has been used as a way of achieving the goal of a constant external stimulus, whose perception is altered by factors intrinsic to the nervous system. Although a great deal has been learnt from this approach (Leopold & Logothetis 1996), a number of questions about the perceptual phenomenon are not completely resolved. First, the identity of the alternating percepts has been questioned (Kovács *et al.* 1996; Logothetis *et al.* 1996; Lee & Blake 1999). The classical view is that the picture dominates first in one eye and then in the other eye, with the implication that the switch is from one eye to the other. A more recent view is that the switch is from the picture of one object to the other. This interpretation is supported by the observation that a percept of rivalry

may still be obtained when the pictures presented to left and right eyes are fractured images in monocular view but comprise two whole images only after binocular combination (Kovács *et al.* 1996). In this case, the experience is of rivalry between the two objects, even though neither eye alone ever receives a view of either of the whole objects. Both types of process (eye rivalry and stimulus rivalry) appear to be at work in human vision (Logothetis *et al.* 1996; Lee & Blake 1999).

A second issue is that the switch from one interpretation to the other in the classic binocular rivalry paradigm is not always complete and instantaneous in all parts of the image at the same time. For example, recent observations suggest a dynamic process that sweeps across the cortical coordinates of an image, changing its appearance over time (Wilson *et al.* 2001). These issues about the different functional mechanisms underlying the emergence of rivalrous percepts and the temporal dynamics of rivalry make the phenomenon more complex than it initially seemed.

There is an additional issue in using the binocular rivalry paradigm in an experiment that studies the behavioural responses of non-human species. Although it is possible to train an animal to respond differentially to samples of the two percepts in binocular rivalry, it is not so easy to guarantee that these responses consistently transfer to the rivalrous stimulus. Suppose, for example, an animal is trained to respond differently to the monocular presentation of horizontal and vertical bars. The animal may well transfer this performance to a binocular rivalry paradigm and report faithfully whether the horizontal or vertical bars are predominant. Nonetheless, for human observers there is a perceptible difference between the monocular presentation of horizontal bars and the same set of horizontal bars when they emerge as the dominant figure out of a rivalrous percept. It seems very likely that macaque monkeys would also be able to perceive the difference between rivalrous and non-rivalrous patterns. We cannot know in advance exactly how a difference of this kind might be reflected in the firing patterns of neurons that we would plan to study, or whether the monkey might alter its behavioural strategy, if it can perceive the difference. It is therefore logical to seek alternative paradigms that retain the essence of the binocular rivalry approach with fewer of its complexities.

(b) *Ambiguity in structure-from-motion*

One stimulus that has been exploited is based on the ambiguity of three-dimensional form depicted by motion information (so called 'structure from motion'; Ullman 1979). A transparent cylinder or sphere that is rotating about its axis can be depicted purely by the motion of dots randomly placed on the surface of the object. When the dots are displayed by parallel geometric projection onto a flat surface such as a computer screen, the motion of the individual dots within the plane of the display has a sinusoidal velocity profile (Treue *et al.* 1991). In terms of dot movements on the computer screen, a cylinder rotating around its principal axis has two planes of dots moving in opposite directions, each corresponding to the rear or front surface according to the direction of rotation of the cylinder. Without an additional cue to specify which direction of dot motion on the computer screen belongs to the front or to the rear surface, the direction of rotation of the
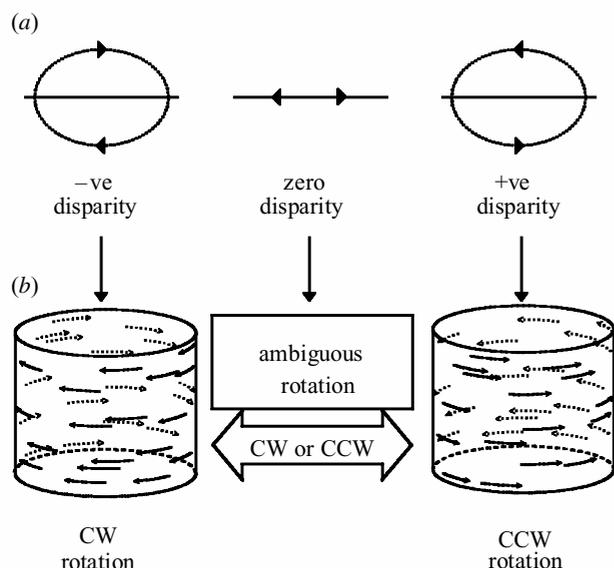
Figure 2. A schematic diagram showing the construction of three-dimensional cylinder stimuli rotating on their axes. The pattern of motion in the dots on the surface specifies the three-dimensional structure of the object. The arrows on the surface indicate the speed and direction of motion of individual dots. When the front and rear surfaces are separated by binocular disparity, the direction of rotation of the cylinder is determined. When the surfaces have the same zero disparity, the direction of rotation is ambiguous but is seen as definitely rotating one way or the other. (*a*) View from above; (*b*) appearance. CW, clockwise; CCW, counter-clockwise.

cylinder is ambiguous, although its speed of rotation and its three-dimensional structure are not. Binocular disparity can provide the necessary cue for disambiguating these stimuli: cylinders in which the front and rear surfaces are clearly separated by binocular depth have a single, unambiguous direction of rotation. Changing the relationship between direction of motion and binocular depth reverses the direction of rotation (see figure 2).

The use of binocular disparity to disambiguate the direction of rotation of these stimuli provides a powerful advantage over binocular rivalry. Small disparities exert a statistical effect, biasing judgements about the direction of rotation, whilst larger disparities can completely fix the direction of rotation. Thus, if a set of different binocular disparities is used, a classical psychometric function for rotation judgements can be built up in which the majority of stimuli have non-zero disparities that separate the front and rear surfaces. This function changes smoothly from 0% clockwise judgements (as viewed from above) to 100% as the disparity is changed. In this paradigm, the ambiguous stimulus with zero disparity lies in the middle of the curve and these stimuli comprise a minority of those experienced by the observer. Crucially, in a single trial the ambiguous stimulus cannot be distinguished readily from an unambiguous stimulus. This leads to a way of checking the integrity or honesty of the subject's judgements about direction of rotation, through monitoring their performance when small non-zero disparities are added to form unambiguous stimuli. This latter point is particularly relevant when an animal has to be trained to give behavioural

responses to report the perceived direction of rotation of the cylinder.

The rotating cylinder stimulus shares one advantage with binocular rivalry: it allows us to probe for evidence of perceptually related signals in areas of the cortex that have already been well characterized in terms of their basic sensory capabilities. In particular, the extra-striate visual cortical area V5/MT contains neurons sensitive to both direction of motion (Dubner & Zeki 1971) and binocular disparity (Maunsell & Van Essen 1983). Since the perceptual resolution of the ambiguous cylinder depends entirely on the specific combination of binocular disparity and motion, there is an obvious case for beginning investigations of this type in cortical area V5/MT. If a neuron is sensitive to the combination of leftwards motion and disparities nearer than the binocular fixation point, then it will respond to an unambiguous vertical cylinder if it is rotating clockwise rather than counter-clockwise. Thus, we are able to generate a tightly controlled experiment on single neurons whose basic sensory properties are relatively straightforward to characterize.

Bradley *et al.* (1998) showed that neurons in area V5/MT respond in a stimulus-driven way to the disparities in the cylinder, often increasing their response monotonically with the disparity of unambiguous cylinders. Moreover, the firing of these neurons reflects not just the sensory characteristics of the stimulus, but also the monkey's perceptual judgements about the direction of rotation of ambiguous cylinders of zero disparity.

Recent work from our laboratory has revealed that the link between the firing of these neurons and the perceptual judgements is in many respects much tighter than initially appreciated. In the first part of this paper, we summarize these findings and present them in the context of other work that has investigated the neuronal basis of perceptual ambiguity. Specifically, we (i) confirm the basic observations of Bradley *et al.* (1998); (ii) show how such results can be expressed quantitatively as choice probabilities (Britten *et al.* 1996; Parker & Newsome 1998); and (iii) demonstrate that the presence of a perceptually related signal is tightly linked to the neuron's sensory capabilities in signalling the direction of rotation of the cylinder. In the second part of the paper, we present the potential links between the presence of perceptually related signals and other modulatory effects upon these neurons, most notably neuronal firing related to changes of attentional state. We also consider the distribution and specificity of these perceptually related neuronal signals across the population of V5/MT neurons. Our aim is to identify the groups of single neurons that are critically involved in perceptual decisions and to study how the formation of perceptual decisions is supported by coordinated activation at the neuronal level.

(c) *Quantitative indices of perceptually related changes in firing*

The basic phenomenon that we need to describe is an association between the firing of a neuron and the perceptual choices of the subject who is performing a psychophysical decision. Each decision is made on a single trial, in response to a single presentation of the stimulus. The structure of such a trial is illustrated in figure 3. Initially, the macaque monkey looks at the fixation target. During
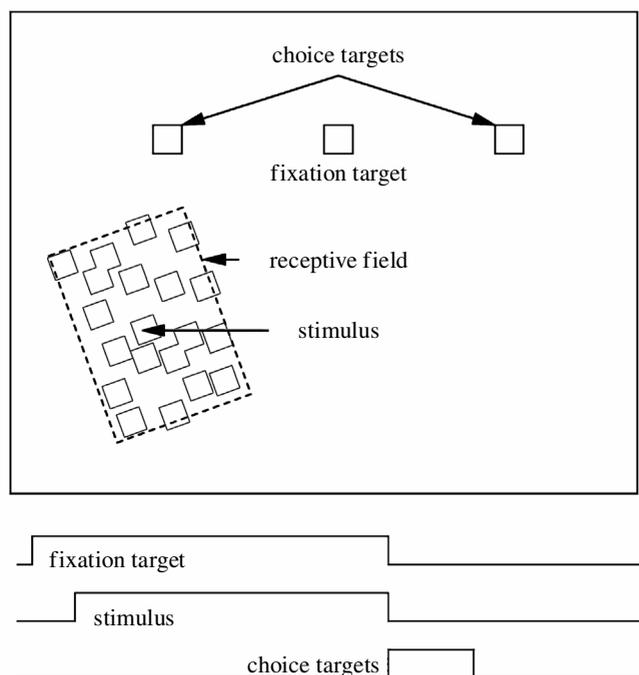
Figure 3. Schematic version of the display viewed by the macaque monkey observer and the sequence of events within a given trial.

this time, a stimulus is presented over the receptive field of the neuron that is being recorded; the basic properties of the receptive field, such as its location, size and stimulus preferences, have been characterized previously. At the end of the stimulus presentation, a decision is required from the monkey in order to obtain a reward. Therefore, the paradigm provides for two choice targets, which the monkey has been previously trained to associate with particular stimulus conditions, such as the left choice target with a clockwise rotation of a cylinder stimulus. The decision of the monkey, the stimulus conditions and the neuronal response are all recorded for analysis. During the analysis, the neuronal activity is sorted according to the decision made on that trial. For some neurons, the activity is stronger when one decision is made rather than another, even though the external stimulus is the same.

Our overall concern in this line of work is to search for evidence about the perceptual relevance of neuronal signals. One way of gathering such evidence, whilst at the same time avoiding the issue of a measurement scale for neuronal activity, is to confine the observations to a qualitative classification of whether there was an increase or decrease in neuronal firing associated with making one choice rather than another. Qualitatively, there is a clear hypothesis to be advanced. Suppose that a perceptual decision is made about an ambiguous stimulus, a decision of the form that a cylinder is rotating clockwise or, for a binocularly rivalrous stimulus, that the stimulus presented to the left eye is currently visible. The suggestion is that we expect the firing rates to be increased in those neurons whose basic sensory preference is for clockwise rotation or for the presentation of stimuli to the left eye. A great deal of valuable analysis can be carried out in this way, purely by inspecting the qualitative correspondence between neuronal preference and the direction of the perceptually related change in neuronal firing (Logothetis *et al.* 1996).

However, decision-related activity is useless as a neuronal signal if it remains anatomically locked in one cortical area and unable to influence other neurons within the brain. Notably, in the cases that we are considering, there must be a link from sensory areas of the brain to those involved with oculomotor control. The biophysical properties of neurons mean that, when one neuron synapses with another, the excitation of the post-synaptic neuron depends, to a significant degree, on whether enough action potentials are fired within a sufficiently short time-period by the pre-synaptic neuron. Therefore, we need to consider the magnitude, as well as the sign, of the neuronal response.

In many areas of science, the choice of a measurement scale for the description of observations often has a profound influence on the conclusions that can be reached from the results. Two different measures of the magnitude of the neuronal response have been explored for the description of perceptually related changes. One of these is to record the increase, or decrease, of activity in terms of the number of extra action potentials associated with a particular decision. Closely related to this are measures such as the percentage change in firing rate: these measures have been used to compare the magnitude of decision-related changes in firing across a large sample of neurons from a particular cortical area (Bradley *et al.* 1998). A significant improvement on measures that are linearly related to firing rate or spike counts is to examine the statistical reliability of the perceptually related change in firing. Measures of this type take account not only of the size of the mean change in firing rate averaged across many experimental trials, but also the trial-to-trial variability of the perceptually related change in firing.

There are two advantages in using statistical measures to describe perceptually related changes in neuronal activity. First, the perceptual decisions themselves have a statistical character, with different decisions being made about the same stimulus over a sequence of presentations. Expressing neuronal activity in statistical terms gives us a common currency for describing both neuronal activity and behavioural decisions. Second, if we wish to understand how groups of single neurons generate psychophysical decisions, then we can use the same common currency to pool the signals from those single neurons in a way that has statistical validity.

(d) *Choice probability*

Britten *et al.* (1996) introduced the concept of choice probability to measure decision-related changes in firing of V5/MT neurons during a task that measured thresholds for the discrimination of motion direction. Choice probability expresses the statistical confidence with which the experimenter can predict the monkey's psychophysical decision at the end of the trial in which an ambiguous stimulus was presented. In the absence of additional information, the experimenter could only make a random choice at the end of the trial about what the monkey would decide. With a binary choice decision (such as 'leftwards' versus 'rightwards' in a motion discrimination task), the experimenter on average would therefore be 50% correct. By taking account of the firing of the neuron that is being recorded at the time, the experimenter can do better than this chance performance. If, on average, the firing of the

neuron is greater when the monkey makes a specific choice (for example, 'leftwards' for the motion task or 'clockwise' for the cylinder task), then the experimenter can improve the prediction rate above 0.5 by analysing the firing of the sensory neuron. At the other extreme, we can conceive of an outcome in which the neuron perfectly predicts the future decision of the animal. In this case, even though there might be some statistical variation in the firing of the neuron, the distributions of firing rates related to the two decisions would be completely non-overlapping. This extreme case of a perfect prediction corresponds to a choice probability of 1.

Previously, we introduced a qualitative classification of the relationship between the sensory preference of the neuron and the perceptually related change in firing. In terms of choice probability, this is expressed by whether the choice probability is below or above 0.5. Choice probabilities above 0.5 indicate that a neuron whose sensory preference is for condition A rather than B also increases its firing when the perceptual choice is A rather than B. Conversely, choice probabilities below 0.5 indicate the opposite (somewhat paradoxical) outcome, in which a neuron with a sensory preference for A actually increases its firing when the perceptual choice is B rather than A.

(e) *Perceptually ambiguous cylinders give strong choice probabilities*

In our work, we have combined the use of these statistical measures of decision-related changes in firing with a task in which the monkey was trained to indicate its perception of the direction of rotation of a cylinder stimulus. This combination allows us to express in a much more precise way just how the signals from single neurons lead to the emergence of a particular perceptual state. It also leads to a rational, statistical basis for examining the conjoint activity of groups of neurons.

The detailed calculation of choice probability is shown in figure 4a,b for two neurons. The basic tuning of both neurons is such that their firing rates change monotonically as the binocular disparity between the front and rear surfaces of the cylinder is altered. As shown in figure 2, negative disparities correspond to clockwise rotation of the cylinder and positive disparities to counter-clockwise rotation. The psychophysical responses of the macaque monkeys are also shown. Note that the psychophysical sensitivity to binocular disparity as measured within this paradigm is excellent. Only tiny amounts of separation by disparity, in the neighbourhood of the threshold for the binocular discrimination of depth differences (Prince *et al.* 2000), are required to disambiguate the direction of rotation of the cylinder.

The analysis of choice probability concentrates on the trials in which all the dots in the cylinder had zero disparity. Figure 4a(ii),b(ii) show the neuronal impulse counts for these trials, coded with different symbols to indicate the monkey's psychophysical response in each trial. For the responses of the neuron in the figure 4a(ii), impulse counts are generally higher when the animal reported that the ambiguous cylinder was rotating in a clockwise direction. The two groups of impulse counts form two statistical distributions, whose separation can be measured by non-parametric methods from ROC analysis (Green & Swets 1966). Beginning with the highest impulse count

and proceeding to the lowest, for each value of spike count (designated 'crit'—criterion level) in figure 4, the probability of achieving that spike count is plotted on the ordinate for the trials in which the monkey's response was clockwise ('pref', thus in concordance with the sensory preference of the neuron) and on the abscissa for the trials where the response was counter-clockwise ('null', in opposition to the sensory preferences of the neuron). Where there is a difference between the firing rates associated with the two choices, the plot shows a consistent deviation away from the positive diagonal towards the top-left corner, as seen for the neuron in figure 4a(iii). The area under these solid curves is the choice probability: for the neuron in the figure 4a(iii), this has a value of 0.67, close to the average for the population.

Figure 5 summarizes the measurement of choice probability in the cylinder task for a sample of 93 neurons from cortical area V5/MT in two macaque monkeys (Dodd *et al.* 2001). The average choice probability is 0.67, considerably greater than a random value of 0.5. This value is also considerably greater than the value of 0.56 reported in the same brain area by Britten *et al.* (1996) for their motion discrimination task. The filled parts of the histogram indicate those neurons for which the measured choice probabilities were individually significant in a bootstrap test (at $p < 0.05$).

Note that figure 5 shows no neurons with statistically significant choice probabilities lower than 0.5. This is in marked contrast to the earlier work of Bradley *et al.* (1998), in which many neurons appeared to show the paradoxical effect of increasing their firing for perceptual choices that are the opposite of their basic sensory preference. The reasons for this discrepancy are discussed in detail in Dodd *et al.* (2001), but the chief differences lie in the statistical treatment of the data and, most significantly, in the fact that in our study the monkeys were working close to the psychophysical limits of performance.

3. THE COMPOSITION OF THE DECISION POOL

For the present discussion, we will refer to the set of neurons that exhibit a decision-related component in their firing as the decision pool, and contrast this set of neurons with those neurons that carry sensory information relevant to the cylinder task, which we will refer to as the sensory pool. The results in figure 5 indicate that the decision pool is defined rather exactly as a subset of the pool of sensory neurons. Only neurons whose receptive fields carry accurate sensory information for judging the direction of rotation of unambiguous cylinders also carry the decision-related component of neuronal activity when ambiguous cylinders are viewed. This is demonstrated by the fact that there are no significant choice probabilities below 0.5 in figure 5. Moreover, for the small number of neurons that had no definite sensory tuning for the direction of rotation of the cylinder, we also found that none of these exhibited a choice probability significantly different from 0.5 (two-tailed test).

This conclusion, that choice probability is highly specific, is in sharp contrast to the previous conclusions with the cylinder stimuli in cortical area V5/MT (Bradley *et al.* 1998). It is also distinct from the pattern of results reported for binocular rivalry (Leopold & Logothetis
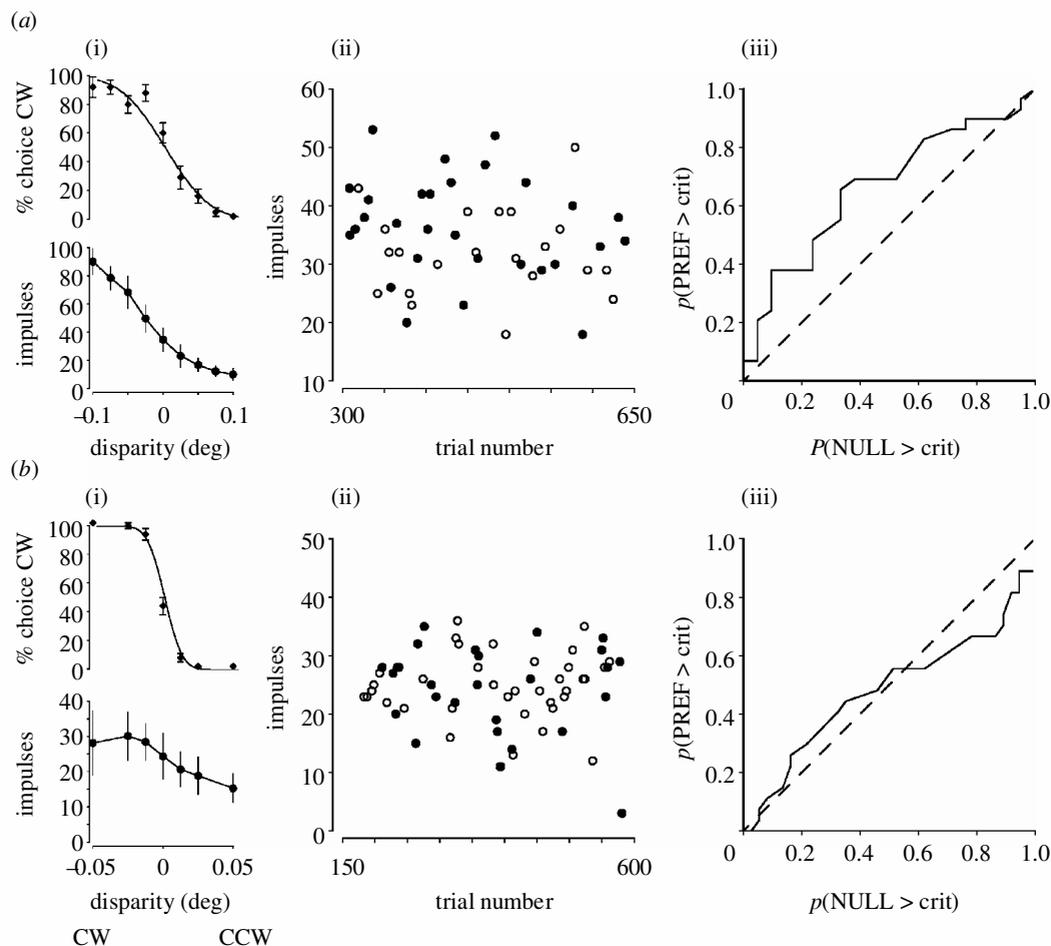
Figure 4. The calculation of choice probability for two individual neurons (see text for explanation). (a) Neuron with a choice probability of 0.66, close to the average for the population. (b) Neuron with a choice probability of 0.48, close to 0.5 and showing no decision-related firing. (a)(i),(b)(i) psychophysical performance (% choice CW) and neuronal activity (impulses in a 2 s period) against disparity of cylinder (see figure 2). (a)(ii) Fifty trials at zero disparity; 29 CW choice (filled circles) and 21 CCW choice (empty circles.) (b)(ii) Sixty-four trials at zero disparity; 27 CW choice (filled circles) and 37 CCW choice (empty circles). (a)(iii),(b)(iii) For zero disparity trials shown in (ii), ordinate shows probability that a criterion level of neuronal firing is exceeded when the monkey chose CW (pref) and abscissa shows probability that the same criterion is exceeded when the monkey chose CCW (null). For abbreviations, see figure 2.
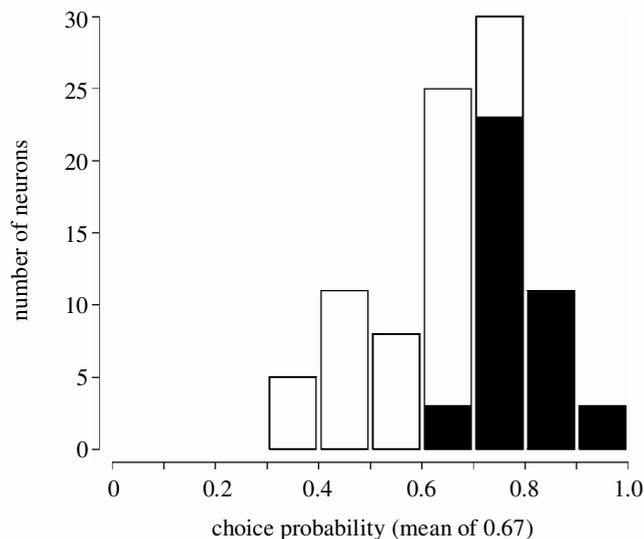

Figure 5. The distribution of choice probabilities for 93 neurons from cortical area V5/MT in two macaque monkeys. Filled histograms: significant $p < 0.05$; open histograms: non-significant. (From Dodd *et al.* (2001).)

1996, 1999; Logothetis *et al.* 1996). In both studies, some neurons showed perceptually related modulations, consistent with their basic sensory response, whereas others showed paradoxical forms of perceptual modulation in opposition to, or apparently unrelated to, their sensory properties. This specificity of choice probability forms the focus of our current work: we aim to define the nature and extent of the neuronal pool within V5/MT that carries signals that relate to perceptual decisions. Our working hypothesis is that perceptual modulation is indeed linked tightly to the underlying sensory properties of the neurons.

(a) *Choice probability and pool size*

The size of the choice probability in the cylinder task is in itself a valuable indicator of the nature and size of the neuronal decision pool. The remarkable aspect of the size of the measured choice probability is quite simply that, when searching with a microelectrode within V5/MT, it is common to encounter neurons whose firing is strongly predictive of the decisions of the monkey. Consider briefly the proposition that statistical variations in the firing of the neurons are uncorrelated between one neuron and its neighbours, and that these variations determine the fluc-

tuations in the psychophysical reports of the monkey. In this case, if we were to observe a choice probability of 1 when recording from a neuron, then we must have been recording from the only neuron in the V5/MT region of the cortex that shows a significant choice probability. The neuronal pool size involved in the perceptual decision would be 1, and we would have been extraordinarily lucky as experimenters ever to record the activity of just that particular neuron. Let us move away from this extreme by just a small step. Suppose that rather than a pool size of 1, we have a pool size of two neurons, with the proviso that in each particular trial only one of these two neurons (at random) carries a decision-related signal. In those trials, where the neuron does carry the decision-related signal, then the signal is statistically unambiguous; in trials when the neuron does not carry the decision-related signal, we would be forced to guess at random the future decision of the monkey. In this case, the measured choice probability would be 0.75 (comprising 50% of trials when the neuron's signal is wholly accurate and 25% where we succeed due to chance). With three neurons, the predicted choice probability would be 0.66, a value close to the mean of the experimentally observed distribution shown in figure 5.

These hypothetical considerations make two points very clearly. First, the assumption of a zero correlation between the neuronal signals is highly unrealistic. Rather, there is likely to be a strong degree of correlation within the neuronal population. Nearby neurons that share inputs from the source of the decision-related signal will tend to fire simultaneously, either because those neurons all receive the decision-related signal or simply because they have strong local interconnections with each other. Second, owing to the correlation between neuronal signals, the presence of a high choice probability from a particular neuron is unlikely to mean that this individual neuron has a unique or highly specialized role in forming the perceptual decision. In our most recent work, we examine these conclusions in detail.

(**b**) *Interneuronal correlation*

It has been recognized for some time that correlated firing within a pool of sensory neurons has significant consequences for the ability of a neuronal population to support the making of perceptual decisions (Johnson *et al.* 1973; Parker & Newsome 1998). Significant gains in sensitivity to weak sensory stimuli could potentially be achieved by averaging the activity of many neurons, but the presence of correlations in neuronal firing means that such gains are limited by the degree of interneuronal correlation. At the extreme, where the statistical variability is completely correlated between all neurons, there are no gains at all from averaging the activity of multiple neurons. Correlated variability between neurons therefore limits the sensitivity of the neuronal pool to weak sensory signals. Equivalently, this means that for a particular level of neuronal sensitivity, larger neuronal pool sizes are required to sustain a particular level of psychophysical performance when there is a modest degree of interneuronal correlation (Shadlen *et al.* 1996).

The model of Shadlen *et al.* (1996) proposes a link between three parameters: the degree of interneuronal correlation, the neuronal pool size and the sensitivity of

individual neurons within the pool to the externally presented sensory stimulus. Within the model, these three parameters govern the predicted level of two additional experimental measures: the choice probability and the behavioural, psychophysical sensitivity of the animal to the sensory stimulus. This model was developed to understand the discrimination of the direction of movement of weak motion stimuli. As already noted, in this paradigm, the choice probability measured within V5/MT for random dot motion stimuli is 0.56 (Britten *et al.* 1996), much closer to 0.5 than the value of 0.67 for the cylinder task studied here. For the stimuli used in the direction discrimination task, Zohary *et al.* (1994) measured the interneuronal correlation as 0.19. We also found values very close to this, using similar stimuli within our experimental set-up (Krug *et al.* 2000*b*, 2001).

Consistent with the predictions of the Shadlen model, we find that when the choice probability is higher, the interneuronal correlation with the cylinder stimulus is also higher. When estimated by measuring the correlation between the activity of a single neuron and the activity of its near-neighbours (recorded as multi-unit activity), the interneuronal correlation in the cylinder task is as high as 0.44 for cortical sites where the stimulus preferences of the single-unit and multi-unit responses are closely matched (Krug *et al.* 2000*b*). However, it should be noted that the large values of choice probability and interneuronal correlation found for the cylinder task place our data outside the range of parameters that have been explored thoroughly in the model of Shadlen *et al.* (1996).

(**c**) *Signals entering the decision pool*

The nature of the signals that enter the decision pool is a topic of some debate. One view arises out of the development of a theory of the origins of choice probability (Shadlen *et al.* 1996). Here, it is thought that the decision signal arises owing to fluctuations in the firing patterns of sensory neurons within V5/MT, or neurons that project there. The decision on each trial is essentially driven by the exact level of activation of sensory neurons in V5/MT, so the trial-by-trial psychophysical decisions are sensitive to the trial-by-trial fluctuations in neuronal firing. This mechanism is the source of correlation of neuronal activity and psychophysical decision. This view of decision-related effects in neuronal firing is essentially a so-called 'bottom-up' view, in which fluctuations early in the sensory process form the limit on psychophysical performance (Barlow & Tripathy 1997).

However, for extra-striate cortical areas, attentional modulation of cortical signals needs to be taken as a serious possibility in the context of perceptual decisions about ambiguous stimuli. Specifically for cortical area V5/MT, perceptually related modulations of firing have been attributed both to perceptual effects (Britten *et al.* 1996; Bradley *et al.* 1998) and to attentional effects (Treue & Maunsell 1996, 1999; Treue & Trujillo 1999). The attentional effects largely take the form of changes in the gain of the stimulus-induced response. Thus, when the animal is attending to a location covered by the neuron's receptive field or to a stimulus feature normally signalled by the neuron, the response of the neuron is enhanced multiplicatively.

The obvious question is whether the changes of firing rate are brought about by manipulating attention and

those that are linked to the eventual decision of the animal are the same phenomenon. Arguably, the decision of the animal in a choice probability paradigm might be formed early in the stimulus presentation. In the case of a completely ambiguous stimulus, which has no correct answer, it might be that the animal's response is dominated by a perceptual bias that is set up even before the stimulus is presented. The bias would persist through the stimulus presentation specifically on ambiguous stimulus trials, because in those trials the stimulus does nothing to alter the initial perceptual bias of the animal. If such a bias were in reality to consist of a shift of attention towards the expected stimulus configuration, then the effect of choice on neurons in V5/MT might be explained entirely in terms of an attentional effect. Note, however, that if attention is involved, the effects of choice on neuronal firing could be accounted for only by feature-based effects of attention, not spatial effects.

Of course, this argument was considered in the earliest choice probability papers (Celebrini & Newsome 1994; Britten *et al.* 1996). Here, the main line of argument for rejecting this possibility was the lack of an effect of choice on firing rates in the pre-stimulus period, before the stimulus was physically present. Since attention has been reported to enhance firing rates for this pre-stimulus period, particularly in cortical areas other than V5/MT, it was argued that attention was unlikely to be the only source of the choice-related effects. However, if the effect of attention is primarily a change in the gain of the stimulus-related response, this line of argument becomes much weaker.

It is reasonable to question whether feature-based attention might be a sufficient account of the choice-related effects observed in V5/MT. At least, it must be accepted that the present designs of experiments in this area allow this as a theoretical possibility. Moreover, the size of some of the attentional effects reported from V5/MT (Treue & Maunsell 1999) would be sufficient to account for the decision-related effects that are being discussed here.

Are there any indications that might guide our thinking? One distinguishing characteristic of an attentional process is that it should reflect, to some degree, the expectations of the observer. An instruction to attend to a target, whether delivered verbally or signalled by a contingency in the experimental paradigm, clearly should have some influence on a process that claims to have some relationship with the neural mechanisms of attention. Of course, it is always possible for attention to be subsequently diverted, but at least the initial direction of attention should be present.

In the course of our experiments on choice-related firing to cylinder stimuli in cortical area V5/MT (Dodd *et al.* 2001), we found that the monkey's choice of direction of rotation in a particular ambiguous trial is sometimes influenced by the response given in the preceding trial. Specifically, for one animal, there was a moderate tendency to stick with a successful (rewarded) response. Thus, in a fully ambiguous trial, in response to which there was no correct answer and rewards were delivered randomly in half the trials, the animal had a tendency to choose the same response that it had made in the immediately preceding, *unambiguous* trial. This is a pattern that has

been characterized as 'win, stay', by analogy with the behaviour of some human gamblers.

This pattern of behaviour might add considerable complexity to the analysis of choice probability. Accordingly, we examined the size of the measured choice probability separately for trials with ambiguous stimuli that were preceded by the two possible types of preceding unambiguous trial (Dodd *et al.* 2001). Taken over the dataset as a whole, we found that although the decision in the preceding trial had a moderate effect on the animal's choices in the current trial, it had no consistent effect on the size of the choice-related modulation of neuronal firing. Therefore, at least by this *post hoc* analysis, the effect of prior expectation on the decision-related neural activity is weaker than the effect of the ultimate choice made by the animal. The effect of attention on neuronal firing seems unlikely, by itself, to offer a complete account of decision-related activity.

(d) *The decision pool and how it is formed*

Until this point in the discussion, we have assumed that the pool of neurons that carries information about the perceptual decision (as assessed by the presence of a choice probability) is the same as the pool of neurons that carries information about the external sensory stimulus. Indeed, several aspects of the design of the experiment have been arranged to ensure that the search for decision-related changes in firing is confined primarily to 'relevant' neurons—where 'relevant' means those neurons that are well tuned to the binocular disparity of the cylinder stimulus. This assumption that the decision pool is the same as the sensory pool is, however, sustained by important aspects of our data. For example, the absence of significant choice probabilities lower than 0.5 cannot be explained by the selection procedure used to choose neurons for testing, since the selection criterion does not depend upon whether a neuron responds more strongly to clockwise or counter-clockwise cylinders.

Nonetheless, when this issue is investigated in more detail, there is evidence that shows that the relevant decision pools must be formed and dissolved dynamically, so that the simple correspondence of sensory and decision pools appears to break down. Britten *et al.* (1996) addressed the question for the motion discrimination task, chiefly by considering cases in which the stimulus was removed away from the receptive field of the neuron and placed elsewhere in the visual field. In these circumstances, the decision-related component of the neuronal firing was absent. With the cylinder stimulus, we are in a much stronger position to assess these effects, simply because the choice probabilities with an optimally arranged stimulus are so much greater.

Rather than examine the spatial specificity of the decision-related activity, we have concentrated on the featural specificity. This is because the influences that generate the decision-related signal are fundamentally involved in differentiating between two stimulus configurations presented in the same spatial location. The direction of rotation of the cylinder is revealed by the binocular disparity that separates its front and rear surfaces. Accordingly, we have examined whether neurons that show strong decision-related activity in the cylinder task are generally implicated in other perceptual decisions about stereo-

scopic depth. There is already independent evidence for a role of V5/MT in stereoscopic depth perception, based on results with electrical microstimulation (DeAngelis *et al.* 1998) and, very recently, on the observation of measurable choice probabilities in a binocular correlation task (DeAngelis & Uka 2001).

We have applied a test to V5/MT neurons based on their responses to binocularly anti-correlated stimuli (Cumming & Parker 1997). Binocularly anti-correlated random-dot stereograms are created with a random-dot pattern that consists of bright and dark dots on a grey background; the pairing of the dots between the left and right eyes is arranged such that each bright dot in one eye is partnered with a dark dot in the other eye. Under suitable stimulus conditions (Cumming *et al.* 1998), binocular stereoscopic depth perception fails with these stimuli. In both V1 and MST, many binocular neurons respond in a disparity-specific way to binocularly anti-correlated patterns with an inversion of the shape of their disparity tuning curves in comparison with the response to binocular correlation (Cumming & Parker 1997; Takemura *et al.* 2001). Such disparity-specific responses in the absence of a stereoscopic depth percept indicate that these neurons code for a preliminary stage in stereoscopic depth processing.

We reasoned that, if the presence of choice probabilities in the cylinder task was simply an issue of whether a neuron had a 'general purpose' role in stereoscopic depth perception, then there should be an association between the presence of choice probabilities and the type of response to binocularly anti-correlated stimuli. Neurons that show strong inverted responses under binocular anti-correlation should have weak choice probabilities, and those that do not have strong inverted responses should have strong choice probabilities. We are able to reject the hypothesis of an association between these two measures of neuronal involvement in binocular depth perception (Krug *et al.* 2000*a*).

All neurons that carry a decision-related signal in the cylinder task also carry a specific signal about binocular disparity. However, the presence or absence of a general role in the perception of binocular depth, as assessed by binocular anti-correlated stimuli, is not predictive for the presence of a decision-related signal. This is despite the fact that binocular anti-correlation is highly disruptive of psychophysical performance in the rotating cylinder task (K. Krug, B. G. Cumming and A. J. Parker, unpublished data).

At present, we have one clear indicator of the composition of the decision pool that derives from measurements of the fundamental sensory capabilities of the neurons that we have tested. These results are illustrated in figure 6. The ordinate of the figure plots choice probability, as calculated previously. The abscissa plots the neurometric threshold of the neuron (Tolhurst *et al.* 1983; Newsome *et al.* 1989; Prince *et al.* 2000). The data show a substantial correlation between choice probability and neuronal threshold, indicating that those V5/MT neurons with the greatest sensitivity to the stimulus disparity represent the neurons at the heart of the decision pool (since these neurons show the strongest choice probabilities). A correlation of this type is evident in the results of Britten *et al.* (1996), but the relationship there is weaker than the one shown in figure 6.
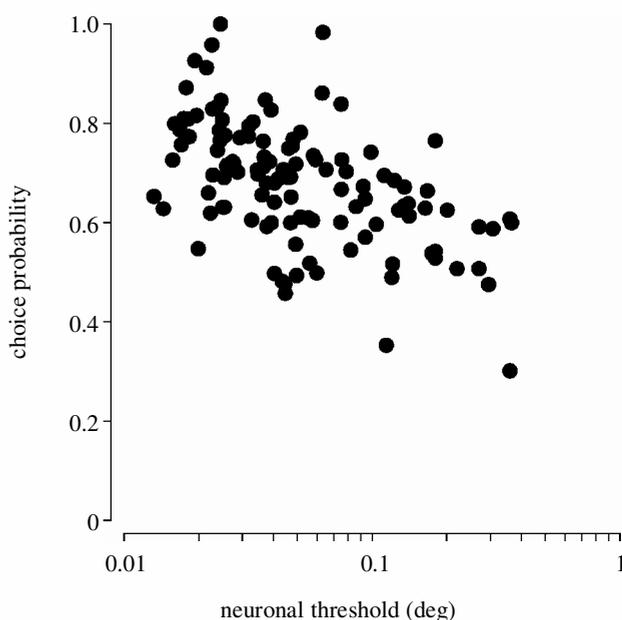

Figure 6. The relationship between choice probability and the neuronal threshold of a sample of 119 neurons from cortical area V5/MT in two macaque monkeys. The neurometric threshold is calculated by applying ROC analysis to the statistical separation of two distributions of neuronal firing, each in response to a different disparity. The neurometric threshold is defined here as the difference in the values of binocular disparity that sustains a separation of the two distributions by one standard deviation. The neurometric threshold is thus high when the neuron is relatively poor at discriminating one disparity configuration from another. The threshold improves if the variability of the neuronal activity is lower and/or a small change in disparity produces on average a large change in response ($r = -0.488$, $p < 0.001$).

Earlier, we observed that all statistically significant choice probabilities are greater than 0.5 and concluded that the decision pool is formed from a set of sensory neurons with quite specific receptive field properties. Here we see that the decision pool has a strong representation only from certain neurons within this set. Neurons with strong choice probabilities for perceptually ambiguous cylinders are those that also have the greatest sensitivity to the disparity signal that is present in the unambiguous cylinder stimuli. Therefore, the decision pool is a tightly constrained subset of the relevant sensory pool.

4. CONCLUSIONS

We have examined how the activity of single neurons relates to perceptual decisions in a well-defined region of the extra-striate visual cortex (V5/MT). The strategy to isolate decision-related activity is to examine the responses to perceptually ambiguous stimuli according to how the monkey classifies them. We can define a decision pool as the set of neurons that show strong perceptually related signals, as measured by choice probability. In many respects, the decision pool is defined by the stimulus preference of the neurons. Decision-related activity is confined to neurons that also signal the presence of one of the configurations of the unambiguous stimulus, in other words, by means of sensory information alone. Decision-related

activity is also significantly linked to the underlying sensory performance of the neurons: neurons with high sensitivity also show high choice probabilities. In our future work, we will examine in more detail the time-course of activity within the decision pool, the temporal relationships between the neuronal activation of members of the decision pool and the important issue of whether the pool of neurons involved in the decision is statically identifiable, as previously assumed, or forms dynamically as the stimulus presentation unfolds. This information will enable us to propose locations for the source of the decision-related signal and understand functionally how and why the signal is generated.

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GLOSSARY

MT: middle temporal visual area
ROC: receiver operating characteristic