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Source: *Philosophical Transactions: Biological Sciences*, Vol. 359, No. 1446, Reviews (Jun. 29, 2004), pp. 929-941

Published by: [The Royal Society](#)

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# A common neuronal code for perceptual processes in visual cortex? Comparing choice and attentional correlates in V5/MT

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In the past two decades, sensory neuroscience has moved from describing response properties to external stimuli in cerebral cortex to establishing connections between neuronal activity and sensory perception. The seminal studies by Newsome, Movshon and colleagues in the awake behaving macaque firmly link single cells in extrastriate area V5/MT and perception of motion. A decade later, extrastriate visual cortex appears awash with neuronal correlates for many different perceptual tasks. Examples are attentional signals, choice signals for ambiguous images, correlates for binocular rivalry, stereo and shape perception, and so on. These diverse paradigms are aimed at elucidating the neuronal code for perceptual processes, but it has been little studied how they directly compare or even interact. In this paper, I explore to what degree the measured neuronal signals in V5/MT for choice and attentional paradigms might reflect a common neuronal mechanism for visual perception.

**Keywords:** vision; perception; extrastriate cortex; attention; perceptual decision; V5/MT

## 1. INTRODUCTION

Since Horace Barlow (1972) postulated that aspects of perceptual awareness should be linked to the activity of single neurons, many correlates for visual perception have been reported (e.g. Britten *et al.* 1992). Neuronal activity is modulated by attention to a particular location or a particular visual feature in numerous visual areas, for example in V2, V4, V5/MT, middle superior temporal cortex (MST) and infero temporal cortex (IT) (see Desimone & Duncan 1995; Maunsell 1995; Treue & Maunsell 1996). Correlates of binocular rivalry have been reported, especially in V5/MT and IT (Logothetis & Schall 1989; Sheinberg & Logothetis 1997). Decision-related activity has been described in V3A, STPp, MST and V5/MT (Britten *et al.* 1996; Bradley *et al.* 1998; Thiele *et al.* 1999; Dodd *et al.* 2001). V5/MT has been implicated in memory storage for moving stimuli (Bisley *et al.* 2001). Electrical microstimulation of neurons in MST affects heading perception (Britten & Van Wetzels 1998). There is evidence for neuronal signals relating to illusory contours and figure-ground segregation in V2, V3 and V3A (Peterhans & von der Heydt 1991; Baumann *et al.* 1997; Zhou *et al.* 2000). Correlates of perceptual learning have been found in IT (Sigala & Logothetis 2002). An abundance of data appear to be available and this list is by no means complete. But variations in methodology and quantification pose a serious problem for direct comparisons of perceptual correlates across different perceptual paradigms and different visual areas. Therefore, I will concentrate on visual area V5/MT.

Area V5/MT has been studied extensively since its discovery in the early 1970s and its neuronal selectivity seems to be much better understood than that of other extrastriate cortical areas (macaque (Dubner & Zeki 1971); owl

monkey (Allman & Kaas 1971)). Most neurons in area V5/MT are direction selective and many are also tuned for binocular disparity (Zeki 1974a,b; Maunsell & Van Essen 1983a). Neurons with the same preference for disparity or direction of motion tend to cluster together (Zeki 1974a; Albright *et al.* 1984; DeAngelis & Newsome 1999), but V5/MT is not only critical for the processing of visual motion and stereo depth, its neuronal signals also influence perception of visual motion and depth directly: electrical stimulation during a direction discrimination and a disparity discrimination task can alter the reported percept in accordance with the stimulus preference of the stimulated neurons (Salzman *et al.* 1990; DeAngelis *et al.* 1998). Whether signals of single neurons in V5/MT represent perceptual processes has been studied in many different ways in the awake behaving macaque (see Parker & Newsome 1998). The gain of a V5/MT neuron is increased when its receptive field (RF) location or a feature it is selective for is attended (Treue & Martinez-Trujillo 1999; Treue & Maunsell 1999). Neuronal signals correlate with the reported percept of ambiguous motion or stereo images (Britten *et al.* 1996; Bradley *et al.* 1998; Dodd *et al.* 2001); electrical stimulation of V5/MT neurons interferes with memory storage for motion (Bisley *et al.* 2001); and binocular rivalry of moving gratings modulates neuronal responses (Logothetis & Schall 1989).

We need to put these perceptual paradigms and the signals that they generate in relation to one another. Studies like those described above are difficult to carry out. In many visual areas, a lack of adequate quantification renders comparisons between variable perceptual correlates rather difficult: one cannot take for granted that behavioural performance was controlled equally tightly or that task difficulty was matched across different studies. Furthermore, to be able to assess the significance of

perceptual signals recorded in single neurons, it is vital to consider whether the signal correlates with the percept in accordance with neuronal selectivity. But in some cases negative and positive correlations with perception are reported for roughly equal numbers of neurons across the visual area, as, for example, binocular rivalry in V5/MT (Logothetis & Schall 1989). By contrast, perceptual choice signals and attentional signals in V5/MT have been intensively studied and appear robust across a large pool of neurons. Much effort has been directed at quantifying these signals, and I will attempt a direct comparison of perceptual signals relating to choice and attentional paradigms to test the hypothesis whether they are manifestations of the same perceptual mechanism. Such a proposal will lead to predictions about the nature of both of these signals.

## 2. CHOICE SIGNALS IN V5/MT

Choice signals are changes in neuronal activity to perceptually ambiguous stimuli, changes that correlate with the reported percept for the stimulus. Thus, they reflect an internally generated signal related to the percept, which is not determined by the visual stimulus. Stimuli that have been typically studied include random motion displays, structure-from-motion cylinders or other bistable images (figure 1*a* and [www.physiol.ox.ac.uk/~kk/stimuli.html](http://www.physiol.ox.ac.uk/~kk/stimuli.html); Britten *et al.* 1996; Bradley *et al.* 1998; Dodd *et al.* 2001). Choice signals are quantified as choice probabilities, which have been introduced by Britten *et al.* (1996). Choice probabilities give the probability with which an ideal observer could predict the subject's behavioural choice by simply comparing trial-by-trial firing rates of two neurons with opposite stimulus selectivity.

Britten *et al.* (1996) recorded from single cells in V5/MT of awake behaving macaques while the animals reported the direction of motion in a random dot display. The motion of the dots was either in the preferred direction for the neuron or exactly 180° opposite to this. At the end of each trial, two choice targets appeared at opposite sides of the motion display along the axis of direction preference for the recorded neuron. The monkey had to indicate its choice of motion direction with an eye movement to the appropriate target. The motion coherence of the random dot stimulus was varied in a pseudo-random order from trial to trial. Some trials were interleaved with zero coherence motion, which contained no net motion signal in any direction. The mean firing rates for all zero motion trials were separated according to choice and the difference between the two distributions of firing rates was summarized as choice probability. The mean choice probability over a population of 299 neurons was 0.56, with even many individual neurons showing a significant correlation between neuronal firing and perceptual report (figure 1*c*).

Neurons in V5/MT are selective not only for direction of motion but also for binocular depth (Maunsell & Van Essen 1983*a*). Thus, they respond selectively to rotating cylinders made up of transparent surfaces of random dots (Bradley *et al.* 1995; figure 1*a*). The direction of rotation of the cylinder is bistable when the depth order of the two transparent surfaces is not defined and they are both at zero disparity (Ullman 1979). In an experiment similar

to that described for the motion stimulus above, primates reported the direction of rotation of such a bistable cylinder while the activity of single cells in V5/MT was recorded. A large choice probability of 0.67 was measured for 93 disparity-selective neurons (Dodd *et al.* 2001; figure 1*b*). Thus, in this paradigm the correlation between the single neuron and the percept appears to be even stronger than for the random motion task.

For both the motion and the cylinder paradigm, investigators found on average a higher mean firing rate when the reported percept resembled the preferred stimulus, and the response was reduced when the null stimulus was perceived. For the cylinder paradigm investigated by Dodd *et al.* (2001), the mean choice probability was higher than for the motion paradigm. This could be due to one very obvious difference between the two stimuli. The cylinder results in a percept that is bistable and fluctuates between two coherent, mutually exclusive interpretations. The average switching time of the direction of rotation is *ca.* 33 s in normal human subjects (Brunskill *et al.* 2003). The random motion stimulus instead simply looks like dots moving in all directions. Thus, for the cylinder the animal reports one of two very different percepts, which appear identical to unambiguous versions of the stimulus, whereas in the motion task the stimuli always appear fundamentally similar and never look like a pattern of dots moving consistently in one direction. This difference in percept may in some way be responsible for the large choice probability.

## 3. ATTENTIONAL SIGNALS IN V5/MT

Single unit (SU) studies in awake, trained animals have demonstrated that the activity of neurons in visual cortex is modulated by selective attention (for review see Desimone & Duncan 1995; Maunsell 1995). This increase in neuronal firing for attended stimuli has been shown to relate to the subjects' performance in a motion detection task and is thought to be at least broadly comparable to an increase in contrast (Cook & Maunsell 2002*a*). All the neurophysiological studies in awake trained macaques that are described here use a cue to direct attention to either a specific location in the visual field or to a particular feature of the visual stimulus.

In V5/MT, attentional modulation has been intensively studied for both of these paradigms. Treue & Maunsell (1996, 1999) compared the responses of V5/MT cells to a moving dot in the RF when the subject was attending either to this dot or to a moving dot at a distant location (figure 2*a*). Both dots were moving back-and-forth while the monkey had to detect a change in speed of the target dot while ignoring changes of speed in the distractor dot. Distractor and target dot could move in the same or opposite directions. Under identical visual stimulation, V5/MT activity was enhanced on average by *ca.* 20% when the monkey attended inside the RF over when attention was focused outside.

Using patches of coherently moving random dots in a similar configuration, Treue & Martinez-Trujillo (1999) reported an increase in peak firing rate of *ca.* 10% for attention to the stimulus in the RF. Both patches of dots always moved in the same direction, thereby excluding any neuronal signals owing to featural attention that might

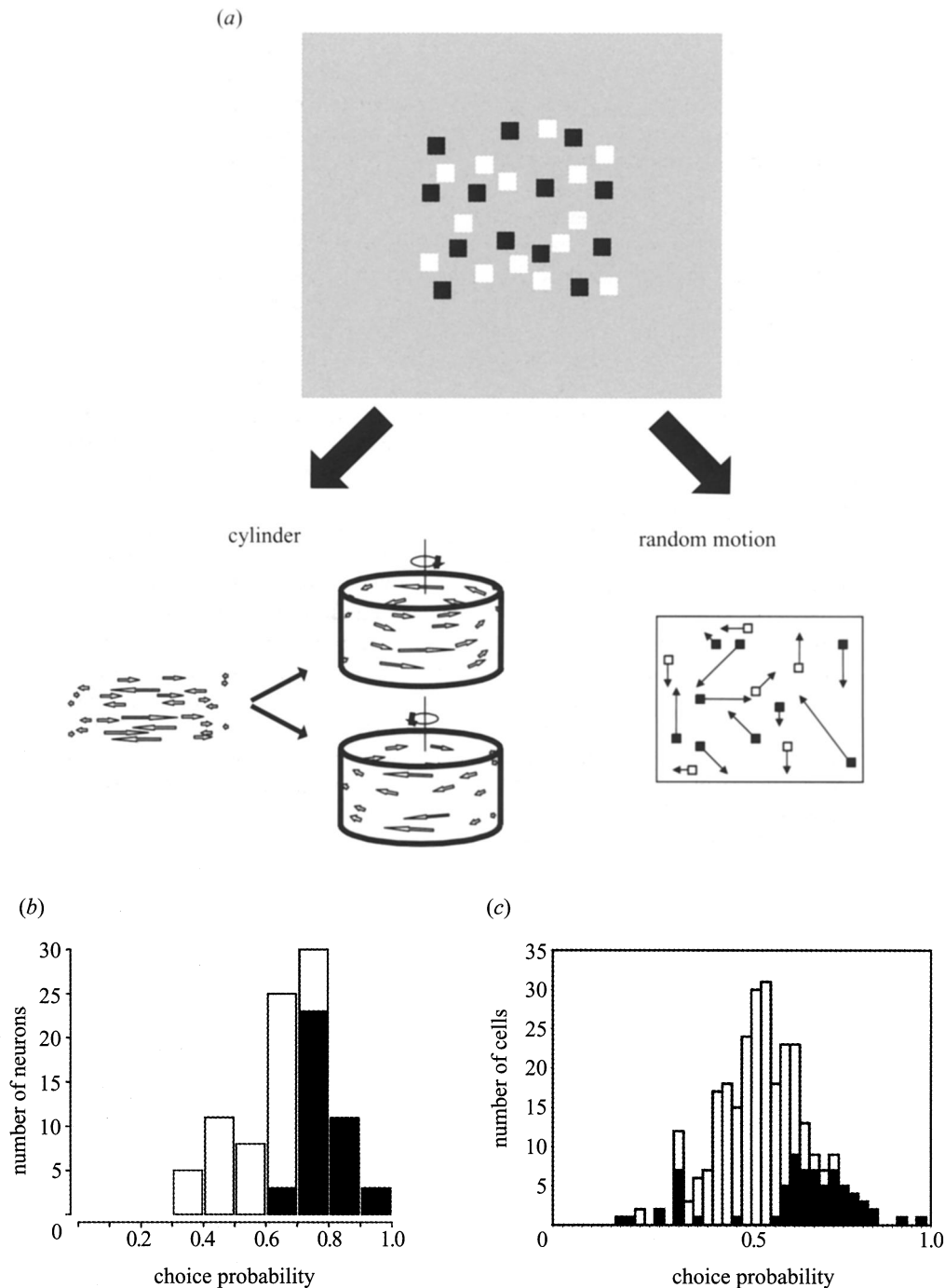


Figure 1. Choice paradigms in V5/MT. (a) A schematic representation of the two stimuli for the choice paradigms. Two superimposed sets of random dots that move in opposite directions with a sinusoidal velocity profile give rise to the coherent percept of a rotating cylinder. The direction of rotation of such a cylinder is bistable and flips at regular intervals. Dodd *et al.* (2001) measured the correlation between a monkey's perceptual choice for bistable cylinders and the activity of single V5/MT neurons. In a motion discrimination task used by Britten *et al.* (1996), random dots were repainted every frame at a random location within the RF. This stimulus appears as dots moving in all directions with no net movement signal in any one direction. The correlation between the reported direction of motion and neuronal firing in V5/MT was estimated as a choice probability. (b) This graph shows the distribution of choice probabilities for the bistable cylinder for 93 V5/MT neurons. The mean choice probability was 0.67 (Dodd *et al.* 2001). These data imply a strong link between neuronal activity in V5/MT and the reported cylinder percept. All significant individual choice probabilities (black bars) were larger than 0.5 (non-significant, white bars). This indicates a positive correlation between the choice signal for the bistable cylinder and neuronal preference for a particular direction of rotation of unambiguous cylinders. (Copyright 2001 by the Society for Neuroscience.) (c) For the random motion stimulus and a direction discrimination task, the mean choice probability was 0.56 for 299 direction-selective neurons (Britten *et al.* 1996) showing a significant correlation between behavioural choice and neuronal activity. Again, most of the significant choice probabilities (black bars) were larger than 0.5 (non-significant, white bars). (Data from Britten *et al.* (1996), with permission.)

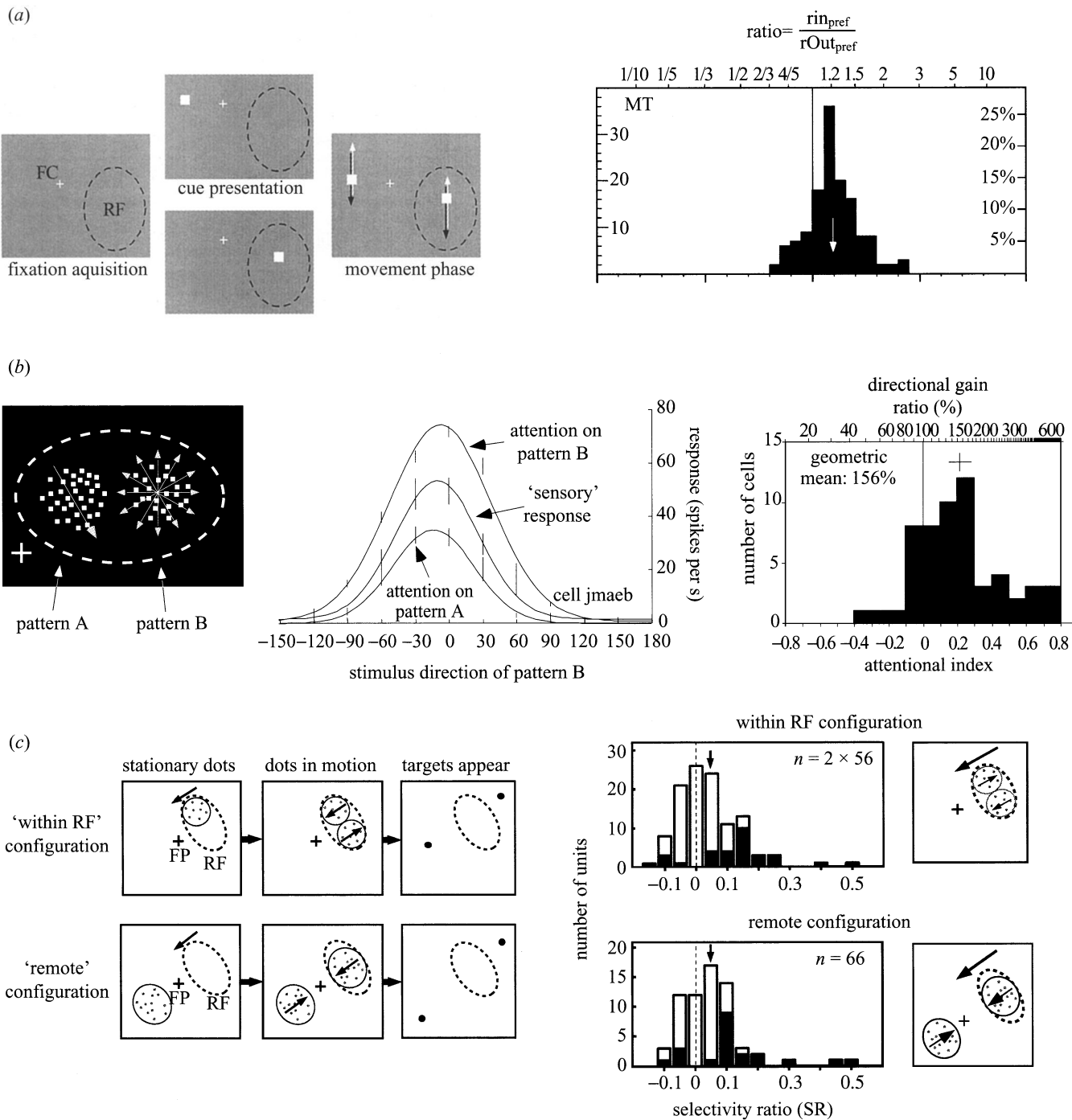


Figure 2. (Caption opposite.)

have enhanced Treue and Maunsell's result. The direction of movement was systematically varied for both patches to study attentional modulation for non-preferred stimuli. The result showed some increase in neuronal response at most directions with attention, indicating a change in gain. Attentional modulation was shown to be much stronger when both a null and a preferred stimulus were present within a single RF and attention was directed to only one of them. Treue & Maunsell (1999) placed two dots with opposite movement directions in the RF, one of which the monkey was cued to attend to. Average neuronal enhancement was *ca.* 70% larger in the time intervals when the monkey attended to a preferred direction of movement for the recorded cell in contrast to when the attended dot

moved in the null direction. An enhancement by 60% was reported for a similar experiment when attention was directed to a patch of random dots moving in the preferred direction against attention directed to a patch of dots moving in the null direction. Both patches of dots were within the RF (Treue & Martinez-Trujillo 1999; figure 2b). The enhancement can be interpreted as a combination of spatial attention (the task) and feature attention (the attentional scoring). Furthermore, in this particular stimulus configuration, competitive interactions between null and preferred responses were seen. Attention to the stimulus moving in the null direction led to a reduced neuronal response (Treue & Martinez-Trujillo 1999; Treue & Maunsell



Figure 2. Attentional paradigms in V5/MT. (a) In this spatial attention task, Treue & Maunsell (1999) placed one moving dot in the RF (dashed outline) and one outside. The monkey had to attend to the dot either inside or outside the RF so as to detect a change in speed in the target dot and ignore changes in the speed of the distractor dot. The attended location was pre-cued by a stationary dot. During the detection task, the dots moved back and forth along the null and preferred direction of the RF. The relative directions of the two dots varied. The histogram on the right shows that the neuronal response was enhanced by *ca.* 20% when the monkey directed his attention to the dot inside the RF rather than outside ( $n = 66$ ).  $\text{rin}_{\text{pref}}$  = average firing rate when the animal attends to the preferred stimulus inside RF;  $\text{rOut}_{\text{pref}}$  = average firing rate when the animal attends to the preferred stimulus outside RF; y-axes: (left) number and (right) percentage of preferred motion epochs. (Copyright 1999 by the Society for Neuroscience.) (b) In this feature attention paradigm two patches of random dots were placed into the RF of a V5/MT neuron (Treue & Martinez-Trujillo 1999). The dots in pattern A always moved coherently in the null direction while the direction of motion for the dots in pattern B was varied for trial to trial (dot coherence 100%). At the beginning of each trial the animal was instructed which patch to attend to so as to detect a change in speed or direction in the target dots. The tuning curves in the middle were plotted for trials when the monkey attended to pattern A, B or outside the RF ('sensory response'). The mean increase in directional gain between attention to the null stimulus (pattern A) and attention to the 'preferred' stimulus (pattern B) was measured as *ca.* 60% in the histogram on the right ( $n = 56$ ). (Copyright 1999 by *Nature*.) (c) Seidemann & Newsome (1999) also measured attentional modulation with two patches of random dots. Either both patches were placed in the RF ('within RF' configuration) or one was placed inside, the other one outside ('remote' condition). Dots moved into the preferred or null direction for the neuron under study and motion coherence was 50–100%. The animal was instructed at the beginning of each trial to which patch it should direct its attention so as to discriminate the direction of motion at the end of a 1 s trial. The within RF and the remote condition yielded a similar increase in attentional gain, *ca.* 9%, when a preferred stimulus was attended to inside the RF against an attended null stimulus inside the RF. (Copyright 1999 by *Journal of Neurophysiology*.)

1999; figure 2b). It is not clear whether this is due to a further withdrawal of attentional gain for the preferred stimulus when the null stimulus is attended or if the reduction is caused by inhibition. Neuronal gain to a preferred stimulus was upregulated by 13% when attention was directed to a preferred stimulus distant from the RF rather than to a null stimulus (Treue & Martinez-Trujillo 1999). This experiment provides an estimate for feature attention while spatial attention was directed somewhere else.

Seidemann & Newsome (1999) used patches of random dots with either 100% or 50% motion coherence. The animal performed a two-alternative forced choice direction discrimination task as in Britten *et al.* (1996) on one of the two patches (figure 2c). The authors compared a stimulus configuration in which both stimuli were within the RF ('within RF') with one where one stimulus patch was outside and one was inside ('remote'). Surprisingly, unlike the previous studies they did not see any increase in the

magnitude of attentional modulation when two competing stimuli were placed within the RF. For both paradigms, attention to a preferred stimulus increased the neuronal response in the range of 6–12%. It is not clear why especially the within-RF condition yielded an attentional gain that was so much lower than the very similar feature attention paradigm by Treue & Martinez-Trujillo (1999).

#### 4. CHOICE AND ATTENTION: TWO DISTINCT PARADIGMS

The question for this review is not whether the experimental paradigms for choice and attention are simply variants of one another, but whether the observed neuronal correlates in both paradigms are caused by identical mechanisms within the brain. The choice experiments cannot be explained in terms of spatial attention because the attention of the observer was for all trials directed inside the RF where the stimulus for the discrimination task was located. This was confirmed through tight behavioural control (Britten *et al.* 1996; Dodd *et al.* 2001). Therefore, spatial attention is always present but should not differ between the two perceptual choices. Theoretically, one could conceive of the choice signals as attentional signals to a particular feature. In the direction discrimination task, the animal could have directed the attention to a particular direction of motion, which in turn would have increased firing rates in neurons that were selective for this direction. Similarly for the bistable cylinder, attention would have been directed on some trials to one particular direction of cylinder rotation and on other trials to the other one. However, the choice paradigms differ in at least three respects from experiments on attention carried out so far.

First, in the choice paradigm subjects were not pre-cued to a particular direction of motion or cylinder rotation. Thus, it is not clear on what basis the animal would 'decide' prior to stimulation which direction to attend to. Both the bistable cylinder and the random motion stimuli are embedded among many trials with stimuli around threshold, which are more or less unambiguous. Therefore, a very strong attentional bias to one direction could potentially impair the animals' performance and reduce their reward. Especially for the random motion stimulus, the psychophysical task seems to be better described, at least the early phases of each trial, as collecting evidence for both perceptual solutions (Britten *et al.* 1996; Gold & Shadlen 2001). Nevertheless, in the cylinder experiments, the history of visual stimulation and reward was implicated in biasing the monkeys' perceptual choice on the ambiguous trials (Dodd *et al.* 2001). In some experiments, monkeys were more likely to choose the same direction of rotation for an ambiguous cylinder as for the immediately preceding unambiguous cylinder, if this stimulus had been rewarded. But analysis across a population of V5/MT cells for the cylinder paradigm showed that such a strategy was not evident in all the experiments. Furthermore, splitting the ambiguous trials by choice on the preceding trial and recalculating the choice probability did not obliterate the choice probability. Therefore, the behavioural bias did not generally account for the choice signal. Similar results have been found for a motion discrimination task and lateral intraparietal (LIP) neurons (Seidemann 1998).

Second, the stimulus in feature attention paradigms generally contains exactly the feature the subject has been instructed to attend to. The attentional modulation is calculated for this defined stimulus feature, which is completely unambiguous. In these paradigms, there is also always a stimulus that needs to be ignored so as to succeed at the set task and obtain a reward. Most choice probabilities are measured for ambiguous trials. In the cylinder paradigm, if we think of V5/MT RFs as being selective for direction of motion at a particular non-zero depth plane, one could argue that the reported feature is not really present in the ambiguous stimulus, because both transparent planes were at zero disparity. Furthermore, no part of the stimulus had to be ignored; the planes of random dots moving in opposite directions form together the cylinder percept and all dots are consumed by the percept.

Third, the choice signal is a direct correlate of the behavioural response on a given trial, because the choice task allows potentially two valid response directions for the bistable stimulus. By comparison, if behavioural performance on an attentional task deteriorated as indicated by the monkey making mistakes, the measured magnitude of the attentional signal would often be lower (e.g. Treue & Maunsell 1999). But the precise relationship between behavioural response and attentional modulation remains unclear, because the set task in those experiments is often used only to assure correct targeting of attention. Thus, it has been difficult to link the size of the attentional modulation to behavioural performance (but see Cook & Maunsell 2002a).

Nonetheless, although there are obvious differences in the design between the two paradigms, this does not preclude that both types of perceptual signals arise by similar mechanisms at the neuronal level.

## 5. TRACES OF SIMILAR MECHANISMS AT WORK

With both attention and perceptual choice, we find that mean firing rates are upregulated in single V5/MT neurons. Is this modulation of the neuronal response implemented in similar ways?

### (a) *Magnitude of the perceptual signals*

First, we should compare overall modulation of the sensory signals by attention and choice. Britten *et al.* (1996) report that the 299 direction-selective cells in their sample fired on average *ca.* 7% more on trials when the animal reported the neuron's preferred direction of motion (across different stimulus conditions). The size of the choice signal for the zero-coherence motion condition alone was not explicitly stated in the paper. However, it can be derived by estimating the normalized mean firing rate for preferred and null choices from fig. 11 in their paper (or figure 4a). The modulation is calculated as the difference between preferred and null responses over the null response, analogous to attentional modulation. But it is important to note that this figure comprises only neurons with significant choice probabilities. The result is a modulation by choice of *ca.* 20% for the zero-coherence motion stimulus alone for cells with a significant choice effect. Calculated in the same way, the modulation by choice for the cylinder stimulus is *ca.* 38% for cells with significant choice probabilities (Dodd *et al.* 2001, fig. 13).

These figures reflect the different mean choice probabilities measured for the random motion and cylinder stimuli.

For V5/MT, spatial attention in and out of a RF that contained a preferred stimulus modulated neuronal firing on average by 10–20% (Treue & Martinez-Trujillo 1999; Treue & Maunsell 1999). Attention to the preferred direction of motion inside the RF increased mean firing rate by 60–70% in comparison to attention to a simultaneously in the RF present null stimulus (Treue & Martinez-Trujillo 1999; Treue & Maunsell 1999). The latter attentional effects are much larger than the choice effects described above, even if one only takes into account the significant choice effects. A much smaller attentional effect was reported by Seidemann & Newsome (1999): 6–12% modulation for a task in which location was attended. Modulation was measured between attended preferred and attended null direction for the recorded neuron as in the previous feature attention task. The attentional effect was the same whether attended and unattended locations were both inside the RF or one was outside.

Stimulus, task and magnitude of the perceptual signal in Seidemann & Newsome (1999) were very similar to the choice paradigm of Britten *et al.* (1996). As usual for attentional paradigms, only trials with a correct choice were included in the analysis, but a correct choice for an attended preferred stimulus is always a choice in the preferred direction of the neuron and vice versa. Therefore, the scoring of the effects is very similar to the choice experiments. There is also a reversal in the sign of the attentional modulation on error trials. For a trial where attention is cued to the 'null' motion patch, this would be a 'preferred' choice, so again the reversed effect we see is consistent with a choice effect. However, choice alone cannot explain some of the perceptual effects seen in the 'remote' stimulus condition (figure 2c for stimuli), which are clearly attentional effects. Also, the time course of the attentional modulation appears very different from the time course of the choice effect in the motion discrimination task (figure 4a,c).

Seidemann and Newsome's experiments also differed from Treue & Martinez-Trujillo (1999) in other ways. The task in Seidemann & Newsome (1999), like both choice paradigms, had a specific endpoint (in this case after 1 s) with at least a 50 : 50 chance of making a correct response, whereas in the other two attentional paradigms (Treue & Martinez-Trujillo 1999; Treue & Maunsell 1999) a random guess would have yielded a much lower probability of obtaining a reward for a correct response. Therefore, these tasks demand attention throughout the trial, which should also increase the mean attentional modulation over the trial. Some circumstantial evidence of how overall task demand might affect psychophysical performance and perceptual signals at the same time stems from work with the bistable cylinder. Reported choice effects were generally higher when the control trials were near behavioural threshold (Dodd *et al.* 2001), whereas smaller choice effects (and negative correlations between choice signals and neuronal selectivity) were observed when interleaved trials contained cylinder stimuli with large binocular disparities (Bradley *et al.* 1998; Grunewald *et al.* 2002). In the latter studies, animals also

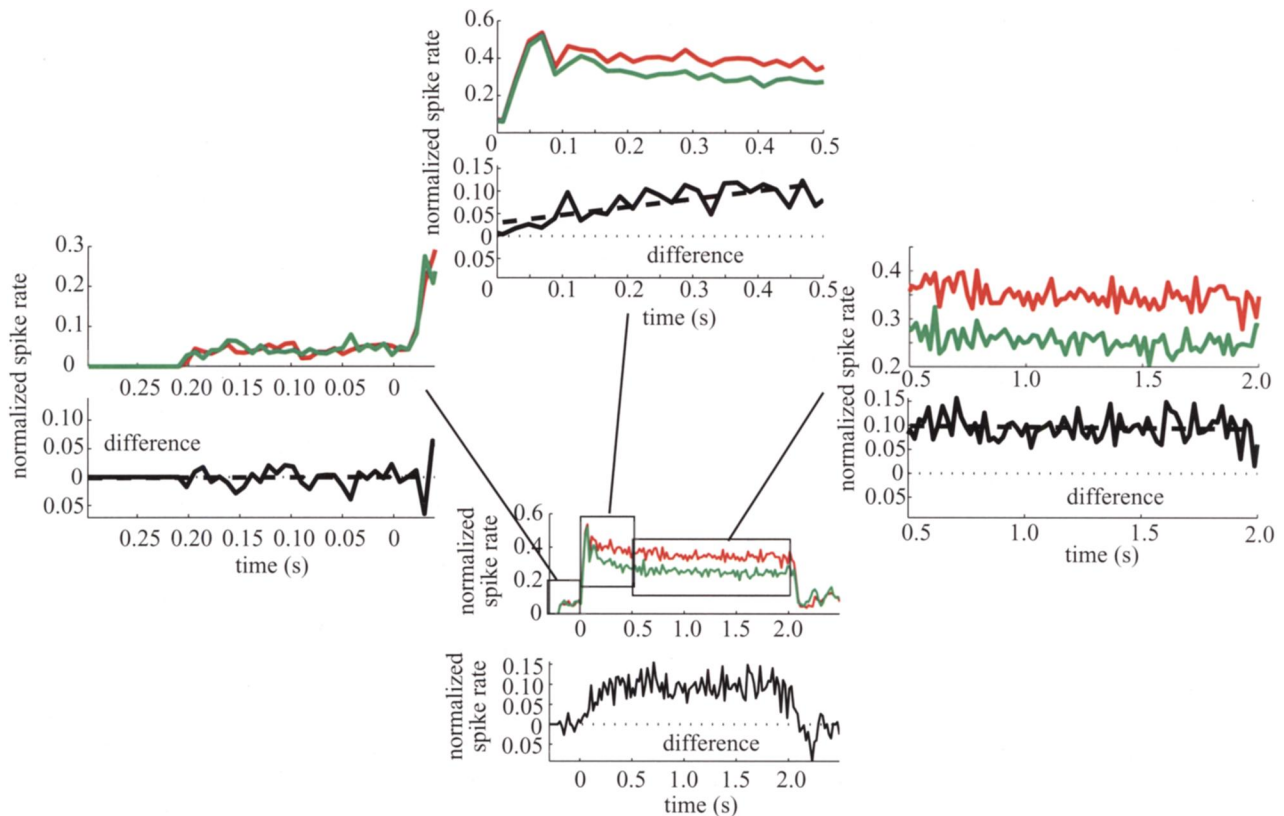


Figure 3. Time course of choice signal for the bistable cylinder. The bottom-centre graph summarizes the time course of the neuronal response across 58 cells with significant choice probabilities in three monkeys (Parker *et al.* 2002a). For each cell, peristimulus time histograms (PSTHs) were constructed separately for choices corresponding to the cell's preferred (red lines) or null (green lines) direction of rotation (bin width 20 ms). For each cell, the pair of histograms was normalized to the peak of the preferred response. The three graphs above highlight different time periods. First, on the left, the pre-period displays no difference in neuronal signal according to choice on the current trial, at a time when the monkey is already fixating but prior to stimulus onset. The graph in the middle shows that the difference in neuronal firing by choice rose steadily over the first 500 ms. This difference remains stable during the final 1500 ms of the trial.

displayed psychophysical thresholds up to an order of magnitude higher than reported in Dodd *et al.* (2001).

Thus, across all the different studies, the range of neuronal modulation by perceptual choice and by attention is at least broadly comparable. The data presented are at least so far consistent with a sliding scale of perceptual modulation that could be controlled by task difficulty and timing.

#### (b) *Specificity of the perceptual signals*

To be able to interpret perceptual modulation in a straightforward way, it has to be linked to the relevance of the neuron to the task. In other words, the potential contribution the neuron makes to perception should be qualitatively similar whether the input to the neuron is driven mostly by sensory input or by perceptual signals. This was not the case for binocular rivalry with moving gratings in V5/MT: many neurons showed significant negative correlations between reported percept and neuronal selectivity (Logothetis & Schall 1989). But most of the significant choice effects for the random motion paradigm were in accordance with neuronal selectivity for unambiguous motion stimuli (Britten *et al.* 1996; figure 1c), as were all significant choice probabilities for the rotating cylinder (Dodd *et al.* 2001; figure 1b). Although some cells in V5/MT increased their firing for unattended

locations or null features, the majority seem to respond consistently with the task (see histograms in figure 2).

It is not just the selectivity of the neuron that determines task-relevance but also its sensitivity. Thus, when choice probabilities were compared with neurometric thresholds, a weak correlation was found for the motion discrimination task in some monkeys (Britten *et al.* 1996) and a stronger correlation in the cylinder task (Parker *et al.* 2002b). The case is less clear-cut for attentional paradigms. For instance, Cook & Maunsell (2002a) measured a choice-like effect in a motion detection task for V5/MT neurons. The data indicate that the attentional signal correlates with successful detection of coherent motion in either an attended or unattended location. However, only stimuli of preferred motion direction were used. The question remains whether this attentional effect would also be present in V5/MT neurons if a null stimulus appeared in the RF, and whether the strength of the attentional signals is linked to neuronal sensitivity.

#### (c) *Product or sum?*

Not only the magnitude but also the nature of the neuronal modulation appears to be similar for choice and attentional paradigms. The choice signals for both zero motion and the bistable cylinder are consistent with a multiplicative change in neuronal gain for the sensory



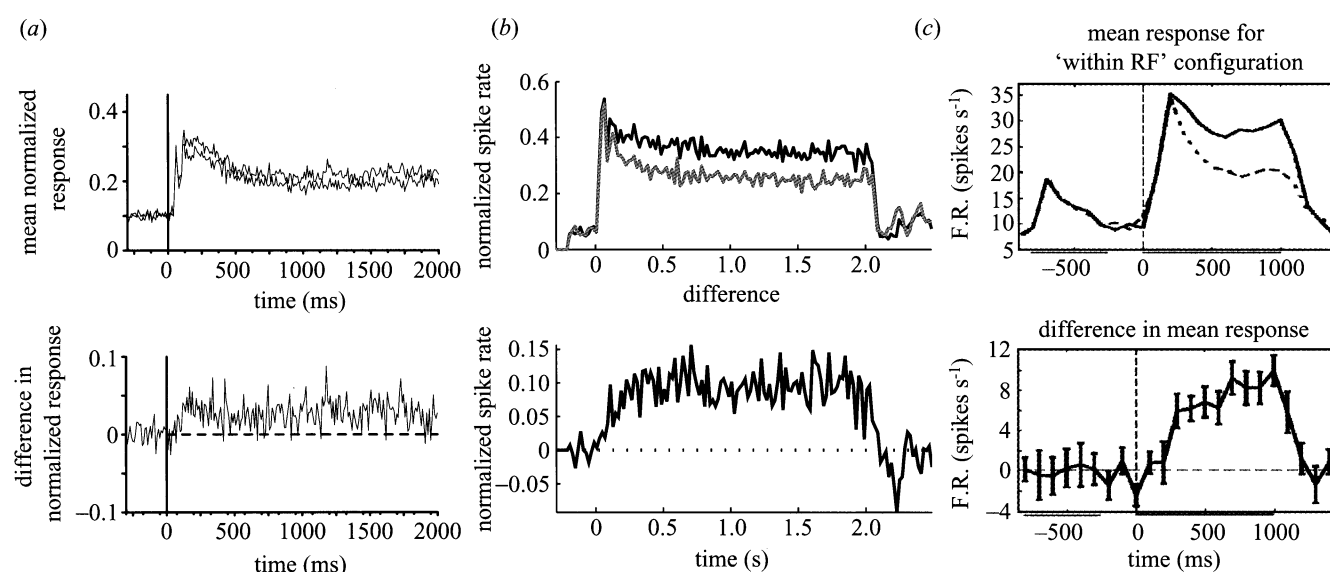


Figure 4. Comparison of time course for different perceptual signals. (a) Britten *et al.* (1996) investigated the time course of the firing rate difference by choice for the random motion stimulus across 75 cells with significant choice probabilities. The responses from each cell for preferred and null choice were normalized to the peak of the preferred direction histogram (bin width 10 ms). The difference in neuronal firing by choice was present almost as soon as the stimulus appeared and it remained stable throughout the trial. (With permission Ken Britten/*Visual Neuroscience*.) (b) This graph summarizes the time course of choice-dependent neuronal firing across 58 cells with significant choice probabilities for the cylinder paradigm (Parker *et al.* 2002a). As described in figure 3, the choice signal arises over the first 500 ms of the trial then remains stable for the remaining 1500 ms. Black line, preferred choice; grey line, null choice. (c) Seidemann & Newsome (1999) analysed the time course of attentional modulation for their 'within RF paradigm' (see figure 2c) for 16 units which displayed a large and significant attentional effect. Average PSTHs were plotted for trials when the monkey attended to the preferred stimulus in the RF (solid line) or to the null stimulus in the RF (dashed line). The difference in attentional modulation began to grow at *ca.* 250 ms and rose steadily until the end of the 1 s trial. F.R., firing rate. (Copyright 1999 by *Journal of Neurophysiology*.)

input rather than an additive signal. For both stimuli, spontaneous rates during fixation but before stimulus onset are the same regardless of whether a null or preferred choice follows on this trial (Britten *et al.* 1996; figures 3, 4a,b). Seidemann & Newsome (1999) reported no attentional modulation in the pre-period (figure 4c). This, however, is not surprising as location within the RF was cued but the attentional effect was measured between preferred and null stimulus. Which stimulus motion would appear at a certain location was randomized. Outside V5/MT, for the majority of studies no modulation with attention prior to stimulus onset has been reported; even a decrease in activity for the attended site has been indicated in V4 (Ghose & Maunsell 2002).

Selective spatial as well as feature attention systematically increased the height but did not affect the width of the tuning curve of V5/MT neurons suggesting a multiplicative effect of attention (Treue & Martinez-Trujillo 1999). Another indication for a change in gain is that attentional signals are competitive. Treue & Martinez-Trujillo (1999) measured direction tuning curves in V5/MT when two random dot patterns were simultaneously placed in the RF (figure 2b), one of which was fixed at the null direction and the other changed its direction of motion. Responses were generally increased by 60% when attention was targeted at the variable stimulus rather than the null stimulus. When the animal carried out a luminance detection task on the fixation point, the tuning curve for the cell lay in between. Thus, one interpretation of this result is that attention to a null stimulus decreases the gain of the neuronal response, again suggesting

a multiplicative event. A recent paper demonstrating a close similarity between V5/MT encoding of contrast and attentional modulation provided further evidence for how attentional signals might effect a change in neuronal gain (Martinez-Trujillo & Treue 2002).

#### (d) Time course

If perceptual signals were to emerge on a similar time-scale in the attention and the choice paradigms, this would provide a further indication of similar neuronal mechanisms. For the random motion stimulus, the choice-dependent differences in neuronal firing rates appeared early in the trials within *ca.* 50 ms and then stayed constant throughout the 2 s trial (Britten *et al.* 1996; figure 4a). Figure 3 shows the time course for the cylinder paradigm in detail (Parker *et al.* 2002a). The larger choice signal for this stimulus emerged more slowly over the first 500 ms of the trial and again remained stable until the end of the 2 s trial. The data presented here differ from Dodd *et al.* (2001), which showed a continuous increase in choice-dependent firing throughout the trial. But this effect seems to have been caused mainly by the data from one animal. With more data and inclusion of a third subject the late rise disappeared (Parker *et al.* 2002a). Thus, for the largest part of the trial, the difference in firing according to choice was stable for both stimuli.

The stability of the choice-related firing over the whole trial might seem surprising at least for the random motion stimulus, given that one interpretation of the choice signal is that it represents bottom-up noise, whose accumulation at a later stage forms the perceptual judgement (see, for

example, Shadlen & Newsome 2001; Gold & Shadlen 2003). But the traces in figures 3 and 4 were averaged over many trials and cells, which would smooth fluctuations in firing that occurred at different times. For the cylinder stimulus, the stability of the choice-dependent difference in firing could more straightforwardly reflect the stability of the percept over this period. If the choice signal were due to a recurrent feedback signal, such a signal could regulate the weight of the bottom-up input to V5/MT and thus keep neuronal activity stable even for the random motion stimulus.

The difference in build-up of the choice-related firing might point at a difference in mechanism. It has been argued before that top-down feedback should emerge on a slower time-scale than a bottom-up perceptual signal (Britten *et al.* 1996; Shadlen *et al.* 1996). Choice signals are inherently very noisy, because their measurement can potentially be affected by many factors, for example behavioural performance. Therefore, the relatively small magnitude of the random motion choice signal mixed with these other factors might render it difficult to assess its emergence accurately.

There are unfortunately fewer data on the time course of attentional signals in V5/MT. Some data suggest that for spatial attention the effect in V5/MT is fairly constant throughout the trial, as long as a stimulus is present (Cook & Maunsell 2002*b*). However, the data are difficult to interpret because the signal to be detected could be in the unattended as well as the attended location; thus the subject could very reasonably have diverted some attention outside the RF. A different result has been described for an attention signal measured for V5/MT neurons during a direction discrimination task (Seidemann & Newsome 1999; figure 4*c*). The authors found a slow time course in the within RF configuration (see figure 2*c*). The increase in neuronal response for attention to the preferred motion direction appeared after *ca.* 250 ms and then grew throughout the 1 s trial. Because the length of the trial was half that of the choice paradigms, the result may be comparable to the time course of the cylinder choice signal (figure 4*b*), but it appears very different from the motion choice signal (figure 4*a*).

The difference between the time courses of attentional modulation obtained by Seidemann & Newsome (1999) and Cook & Maunsell (2002*b*) probably lies in the task design. The latter was a detection task, where the subject might have to respond at various points during a trial, and the former a fixed interval detection task, with a choice only required at the end. Therefore, one explanation for the late rise in attentional modulation in Seidemann and Newsome's data could be due to variability in when the monkeys begin to attend to the task. Indeed, Ghose & Maunsell (2002) have shown, for neurons in V4, that the timing of events in the task can have a profound effect on the time course of attentional signals. Another possibility is that attention and choice signals interacted in varying ways throughout a trial. Spatial attention should have been the same whether the monkey made a null or a preferred choice. However, the animal could enter each trial with an attentional bias for (or an expectation of) a particular direction of motion, manifest as a feature attention signal in V5/MT. This bias would be on some trials in the same direction as the direction of motion in the sensory

stimulus; on other trials it would contradict it. Only correct trials were included in the time-course analysis and data separated by the presence of a preferred or a null stimulus in the RF. Thus, towards the end of each trial, the neuronal response would be almost exclusively modulated by 'the choice' for the preferred or the null stimulus. With such a scenario, the time course of the perceptual signal would also be rising slowly over the trial. Because the task in Seidemann & Newsome (1999) closely resembled the one in Britten *et al.* (1996), an analysis of choice probabilities (which would include the error trials) would be very interesting.

Taken together, at the level of the individual V5/MT neuron, the range, timing and nature of the neuronal modulation for choice and attention could be related. Many of the differences we saw could easily be explained by variations in task demand. But if these perceptual signals are generated by similar mechanisms, they should stem from the same source.

## 6. A COMMON SOURCE FOR PERCEPTUAL SIGNALS?

The question remains how perceptual choice and attentional signals are generated. Whether perceptual choice signals are a bottom-up or a top-down phenomenon is quite controversial. The case for the attentional paradigms studied in V5/MT neurons seems more straightforward. We have been looking at paradigms that are pre-cued, either through the actual stimulus to be attended or more abstractly. This is not bottom-up attention capture by salient stimuli in the visual image (like a red apple among many green ones). The attentional modulation in V5/MT is large, can be dynamically controlled through cues and shows competitive interactions within a RF. Feature attention is obviously linked to RF properties, but it has not been established if attentional effects are also linked to the sensitivity of the neuron to the task. Outside V5/MT, it has been shown that attentional modulation can be controlled through abstract cues and can modulate activity over a large area (Motter 1994; Desimone & Duncan 1995; Conner *et al.* 1996). All these are experimental features that suggest a top-down signal, which modulates activity in varying cortical pools tailored to the respective task and its demand (Cook & Maunsell 2002*a*).

What are not clear are the actual source and the level of entry into the visual hierarchy. Seidemann & Newsome (1999) showed no difference in modulation due to spatial location whether two competing stimuli were both inside the RF or one was outside. This might suggest multiple 'levels of entry' to V5/MT and below, where visual RFs are smaller. Recent work by Cook & Maunsell (2002*a*) showed that attentional effects for the same task are distributed throughout many extrastriate visual areas. Attentional modulation grows between early visual areas and later ones. It will be crucial to link these results to neuronal sensitivity for the set task at these levels.

But where in the cortical hierarchy is the choice signal generated? In the original random motion study, based on a substantial theoretical framework, the choice signal has been attributed to a bottom-up signal, where random fluctuations in the responses (intrinsic noise) upstream from V5/MT contribute to the choice signal in a small pool of

neurons (Shadlen *et al.* 1996). The mean choice probability of 0.56 for this motion discrimination task is quite small. It is linked to the sensitivity of the neuron to the task. When the axis of motion in which the monkey had to make his judgement was changed from the RF preference or the stimulus was moved off the RF, neurons either ceased to show a significant choice effect or choice probability was much reduced (Britten *et al.* 1996). It appears that the choice signal is quite tightly linked to a small group of V5/MT neurons with the appropriate RF properties. However, the choice signal is so small that a small change could easily be missed or a small decrease in the measured choice probability could render the choice effect non-significant if only studied in a smaller group of neurons. The stability of the choice-related difference in neuronal firing over the trial could also indicate a bottom-up signal, whereas a top-down feedback signal might only appear some time after stimulus onset and grow over the length of the trial, as data from some experiments with attention suggest (Seidemann & Newsome 1999). But depending on the precise mechanics, there seems to be no reason to presume that a top-down signal could not be stable during a trial; indeed some manipulations of the task for an attentional paradigm in V4 resulted in a fairly constant attentional signal throughout the trial (Ghose & Maunsell 2002).

The case lies quite differently for the large choice probability measured for the ambiguous cylinder (Dodd *et al.* 2001). With 0.67, the choice probability appears too large to be easily explained by a bottom-up signal detection model as proposed for the random motion paradigm. The choice signal seems to be widely distributed across V5/MT columns of different direction preferences (Curnow *et al.* 2002), but it is still broadly linked to the neuronal selectivity for cylinder rotation because there were no significant choice probabilities smaller than 0.5. The strength of the choice signal for the cylinder is correlated with the neurometric threshold of a neuron, and thus its sensitivity to the task (Parker *et al.* 2002b). This is consistent with how an increase in gain should manifest. So far, the cylinder choice signals we measured could be due to a strong top-down signal, which acts on one of two large pools of V5/MT neurons with roughly opposite preferences for direction of cylinder rotation.

The circumstantial evidence presented suggests that random motion and cylinder choice signals could have a different source. The mechanics of the choice effect for bistable cylinders show many similarities with a top-down feature attention signal. Another possible indicator of source for the choice signal is the amount of 'shared noise' between neighbouring V5/MT neurons. The 'shared noise', which is measured as interneuronal correlation of mean firing rates, can be taken as a measure of common input. For random motion stimuli the interneuronal correlation between pairs of V5/MT neurons with the same direction preference has been measured as *ca.* 0.19–0.21 (Zohary *et al.* 1994; Bair *et al.* 2001). When the two neurons have similar RF locations but different direction preference the interneuronal correlation disappears. Interneuronal correlation for random motion seemed to be unaffected by the absence of the discrimination task as well as by the size of the choice probability. This would

be consistent with most of the interneuronal correlation being due to shared bottom-up input.

If we compare this with the interneuronal correlation measured for the cylinder stimulus an interesting difference emerges. In this experiment, interneuronal correlation was measured between a single unit (SU) and its surrounding multi-unit activity (MU). When cylinder stimuli and random motion were interleaved, the interneuronal correlation for the bistable cylinder was significantly larger (0.44) than for the random motion stimulus (0.27; Krug *et al.* 2000). The large interneuronal correlation for the bistable cylinder was not only dependent on matched tuning preferences between SU and MU, it also correlated with the choice probability measured for the SU (Krug *et al.* 2001). Thus, the amount of shared input appeared to change with the choice signal independently of the visual stimulus. These results strongly suggest that the choice signal for the bistable cylinder has a dynamic, top-down component very much like the attentional signals described above.

But what about the source of the choice signal for random motion? There is indeed little evidence in the data presented above for a top-down signal driving behavioural choice, and we would need to conclude that the choice signal for random motion and the bistable cylinder have a different source. However, the random motion stimulus never leads to a coherent and strong percept of motion in one direction (unlike the bistable cylinder), which fits well with a small and localized signal representing the choice. The small size of the choice effect and the level of interneuronal correlation for random motion render it likely that small fluctuations in either of them may have been missed. Because of the similar nature of the two choice tasks, where sensory evidence needs to be evaluated, it seems more plausible that both choice signals have a bottom-up component (as originally proposed for a motion discrimination task by Britten *et al.* (1996)). This could be relatively stronger for random motion and relatively weaker for the cylinder paradigm.

## 7. THE VERY SAME MECHANISM?

The formal structure of the choice and the attentional paradigms is very different in terms of task specification and task demand. However, it is conceivable that at the neuronal level the same mechanism may underlie the perceptual signals observed in these two paradigms. At least for the cylinder choice and the attentional paradigms in V5/MT we find evidence for a strong dynamic signal that is distributed across a group of neurons that could represent the perceptual pool. This signal is manifest in an increase in gain of neurons that are well suited to contribute to the percept. This potential relationship between neuronal firing and reported percept is expressed for the choice paradigm as the choice probability. One major key to address the question whether choice signals and attentional signals in V5/MT employ the same mechanism is how changes in the attentional signal relate to performance in a perceptual task. The other lies in the interactions between attention and choice signals at the neuronal level.

Psychophysical experiments have established that spatial attention improves performance in a detection task (Eriksen & Hoffman 1972; Posner 1980). Recently,



Cook & Maunsell (2002a) investigated whether changes in the neuronal firing of V5/MT neurons with attention directly correlate with the detection thresholds measured. Neuronal modulation by attention in V5/MT can explain some of the subjects' improved performance with selective attention but not all of it. Also, more evidence is needed about the distribution of attentional signals with respect to RF properties and neurons' sensitivity to a particular task.

Cook & Maunsell (2002a) addressed in this study another important question: how attentional signals for the same task are represented on different levels of the visual hierarchy. They compared the magnitude of the attentional modulation at the neuronal level in V5/MT and VIP and related it to modulation of the behavioural detection threshold. The attentional modulation was not strong enough at the level of V5/MT and too large in VIP. They postulated that the brain area(s) that show an approximately appropriate level of attentional gain to explain the improvement of detection threshold would be most likely to underlie the percept. This should also be the area in which neurons show the greatest selectivity for and sensitivity to the relevant visual parameter in the task.

For all the paradigms described, V5/MT appears to be a very appropriate site to process the relevant stimuli, owing to the specialized RF properties and organization. But it is not the only one. V5/MT receives direct inputs from direction-selective neurons in V1 (Movshon & Newsome 1996), inputs from V2, V3, V3A and V4, and projects in turn to MST, FST, VIP and LIP (Maunsell & Van Essen 1983b; Ungerleider & Desimone 1986; Blatt *et al.* 1990). There are also many feedback projections. There is evidence that LIP is already accumulating the perceptual evidence for the motion discrimination task, which is represented in V5/MT, to convert into a behavioural response (Shadlen & Newsome 2001). To study the hierarchical distribution of perceptual signals and especially the time course of their emergence at various levels should aid us in determining their source and the appropriate place in the hierarchy at which to compare choice and attentional signals. However, we might have to look at more than one visual area for each task because the spread of perceptual signals might in turn reflect the distributed nature of visual perception as has been previously proposed in models of multi-stage integration (Zeki & Shipp 1988).

To elucidate whether the same mechanism underlies attentional and choice effects, we also need to investigate the contribution that attention might make to the choice signal. In both the random motion and the cylinder paradigms, we would expect that spatial attention is directed to the stimulus location. But to what extent are some of the observed signals due to feature-based attention to a particular direction of motion or a particular direction of rotation of the cylinder? It appears that the perceptual choice signal is stronger for the more coherent cylinder percept than the random motion stimulus. The smaller attentional modulation has been reported with a somewhat lower coherence stimulus (Seidemann & Newsome 1999). But in all the attentional paradigms described, attention was directed to strong unambiguous stimuli. The pieces of data that are missing from this puzzle are obvious. We need to find out how attentional signals are affected by manipulating stimulus parameters. The nature

of the cue for directing attention becomes important if we want to argue that choice and feature attention derive from the same mechanism. In this case, internal behavioural strategies or attention capture without an explicit pre-cue should exert similar effects on the neuronal level as we have seen for the attentional paradigms using external pre-trial cues.

## 8. FUTURE EXPERIMENTS

A first step should lie in the direct comparison of an attention and a choice paradigm. One candidate would be the motion discrimination paradigm used by Britten *et al.* (1996) combined with the attention paradigm by Seidemann & Newsome (1999), which also uses a direction discrimination task. But the larger choice signal for the bistable cylinder, again paired with an appropriate attentional paradigm, might be a more likely candidate to elucidate small fluctuations in these perceptual signals. To derive adequate data from such a comparison, tight control is needed for task and stimulus. Behavioural performance has to be at psychophysical threshold in all different experimental conditions. Task demand and probability of reward need to be equated. Once this is achieved and if choice and attentional effects are generated by the same mechanism we should be able to find the following:

- (i) time course of attentional and choice signals should be comparable;
- (ii) modulation caused by attention directed to a particular stimulus feature should be measurable for an ambiguous (or suboptimal) stimulus;
- (iii) choice signals should be present for unambiguous stimuli near threshold as long as the animal makes mistakes (some evidence presented in Dodd *et al.* (2001));
- (iv) attentional signal should correlate with performance (some evidence presented in Seidemann & Newsome (1999) and Cook & Maunsell (2002a)); and
- (v) time course and magnitude of perceptual modulation in reaction time tasks should be correlated between the two paradigms.

Ultimately, we must move beyond establishing parallels in cortical processing for the two paradigms and look at interactions between them. The direct effects of manipulating attentional state have to be studied while the animal performs a choice task. Attentional signals could be manipulated, for example, through varying the number or distance of possible targets or through changing stimulus coherence or noise. If feature attention and choice effects change the gain of V5/MT neurons independently, their interaction should be multiplicative. If they stem from the same source, their actions are more likely to be additive. If perceptual signals have a capacity limit, increasing one should adversely affect the other.

I am very grateful to Andrew Parker and Bruce Cumming for their invaluable comments on this manuscript. I thank Ken Britten, who kindly furnished me with figures 1c and 4a, and Tam Curnow, who provided some of the data and the graphs for figure 3. I also thank Andrew Parker, Bruce Cumming and many others, who fought with me over many of the issues raised in this paper.



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