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How do we select perceptions and actions? Human brain imaging studies

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The selective nature of human perception and action implies a modulatory interaction between sensorimotor processes and attentional processes. This paper explores the use of functional imaging in humans to explore the mechanisms of perceptual selection and the fate of irrelevant stimuli that are not selected. Experiments with positron emission tomography show that two qualitatively different patterns of modulation of cerebral blood flow can be observed in experiments where non-spatial visual attention and auditory attention are manipulated. These patterns of modulation of cerebral blood flow modulation can be described as gain control and bias signal mechanisms. In visual and auditory cortex, the dominant change in cerebral blood flow associated with attention to either modality is related to a bias signal. The relation of these patterns of modulation to attentional effects that have been observed in single neurons is discussed. The existence of mechanisms for selective perception raises the more general question of whether irrelevant ignored stimuli are nevertheless perceived. Lavie's theory of attention proposes that the degree to which ignored stimuli are processed varies depending on the perceptual load of the current task. Evidence from behavioural and functional magnetic resonance imaging studies of ignored visual motion processing is presented in support of this proposal.

Keywords: attention; PET; fMRI; visual; auditory

1. INTRODUCTION

Humans have a remarkable ability to attend selectively to one out of many competing streams of information (Cherry 1957; Broadbent 1958). Selection of a stream can be made not only on the basis of modality, but also within a single modality. Furthermore, subjects can attend to a subset of information within a single stream. Such a process, of selecting from among many incident stimuli, is the clearest manifestation of selective attention. This paper will discuss the nature of attentional selection; in particular, the neural mechanisms underlying selective processing and the fate of rejected stimuli. Initially we present a selective review of neurophysiological studies suggesting that there are two different types of extra-retinal signal involved in selection in the visual modality. We then describe functional imaging experiments in humans that suggest that changes in regional cerebral blood flow (rCBF) follow a similar pattern. Finally we discuss recent functional imaging evidence that the degree to which rejected stimuli are nevertheless processed depends on attentional load.

2. MECHANISMS OF SELECTION

(a) *Single neuron*

Moran & Desimone (1985) investigated whether responses of single cells in visual areas differed depending on whether or not a monkey was attending to a stimulus. In primary visual cortex, there was no difference, but in area V4 the response to an irrelevant stimulus was reduced by about two-thirds. Furthermore, this attenuation only occurred when both attended and unattended stimuli were located simultaneously within the receptive field (RF) of the neuron. When the unattended stimulus was outside the receptive field and the attended stimulus inside it, no modulation of neural responses was observed. In inferotemporal cortex (IT), attenuation was always observed, as the receptive fields in this area are large and cover most of the visual field. The effects of attention are invariably seen when both relevant and irrelevant stimuli are presented simultaneously, but effects are also seen when stimuli are presented sequentially, suggesting that competition takes place in both space and time (Luck *et al.* 1997). Desimone & Duncan (1995) argued that these findings were compatible with a 'biased competition' model of attention, where objects in the visual field compete for processing at the receptive field level. The role of top-down selective influences is to bias the processing at a cellular level towards one stimulus or the other. The results of Moran & Desimone (1985) are consistent with this as they show that attention only has an effect when relevant and irrelevant stimuli are competing for the cell's response. According to the 'biased competition' model, perceptual selection is a two-stage process (Desimone & Duncan 1995). Initially, top-down signals bias activity in neurons representing the relevant object or location. Consistent with this, elevations of baseline firing rates are seen in V4 neurons whenever attention is directed towards their receptive field (Luck *et al.* 1997); similarly in IT, neurons show elevated activity in the delay period of a delayed match-to-sample task (Chelazzi *et al.* 1993). These findings are consistent with an

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extrinsic 'bias' signal. In the second stage of perceptual selection, neurons that have received a bias signal gain an advantage in their competitive interactions (mediated through local intrinsic connections) with other neurons. Consistent with this, attention to non-spatial features of objects influences not only baseline (spontaneous) firing rates but also modulates stimulus-evoked responses (Haenny *et al.* 1988; Ferrera *et al.* 1994; Luck *et al.* 1997). Thus it seems that there are at least two different mechanisms at a single-cell level that might mediate selective attention. In visual cortex, elevations in baseline firing rate and modulation of stimulus-evoked activity are two mechanisms that appear to operate.

(b) *Electrophysiological*

Electrophysiological studies in humans are discussed elsewhere in this volume (Hillyard *et al.*, this issue) and will not be reviewed in detail. The most important finding from event-related potential (ERP) studies is that components arising very soon after the presentation of a stimulus clearly differ as a function of whether the stimulus is attended or ignored (Hillyard *et al.* 1995). The visually evoked component P1 is smaller when a stimulus is ignored because of its location. When selection is based on stimulus attributes other than location, such as colour, an additional component is superimposed on the N1 and P1. This colour selection component is substantially reduced when the stimulus is in an ignored spatial location, suggesting that the location and colour selection are organized hierarchically with location-selection dominant (Mangun *et al.* 1993). The location of the generators of these components in early sensory processing areas suggests that the mechanism of selection not only operates very soon after stimulus presentation but also very early in the anatomical hierarchy of processing areas (Woldorff *et al.* 1993). It is difficult to relate these ERP findings to the single cell data, because stimuli in ERP studies are frequently presented alone to aid interpretation of the resultant waveforms. Furthermore, where ERP attention effects have been seen as a function of competition between relevant and irrelevant stimuli, the stimulus conditions have never led to the simultaneous presence of attended and ignored stimuli inside a single receptive field in extrastriate cortex.

(c) *Functional imaging*

In humans, functional imaging studies have shown that attention to different attributes of visually presented stimuli changes evoked activity in areas of cortex concerned with processing those attributes. For example, attention to the colour of visual stimuli changes evoked activity in cortical area V4, compared with attention to the motion of identical visual stimuli (Corbetta *et al.* 1990, 1991). Similarly, attention to visual motion modulates the stimulus-evoked activity in cortical area V5 (Büchel & Friston 1997; O'Craven *et al.* 1997). These functional imaging experiments have demonstrated the general principle that attention modulates functionally segregated and stimulus-specific regions of visual cortex, but have not provided any insight into the mechanism of such processes. The reason for this lies in the experimental design; typically, investigators have compared a state where the subject attends to a certain aspect of a display with a state where the subject receives identical visual stimulation but does not attend. The difference in activity between these two states has been attributed to the effects of attention. However in light of the preceding discussion it can be seen that such a difference between 'attend' and 'no attend' conditions necessarily conflates both additive and interactive (stimulus-evoked) components of attention. Intuitively this can be seen by imagining doing the experiment again but without using a stimulus. Would comparing 'attend' and 'no attend' reveal a difference in evoked activity (that could be produced by a change in baseline firing rates or bias signal), or is such a difference contingent on stimulus-evoked activity (a true modulatory effect of attention)? Such a thought experiment serves to illustrate the theoretical point that to characterize the effects of attention by using functional imaging requires an experimental manipulation of stimulus-evoked activity that is independent of the experimental manipulation of attention. The independent manipulation of attention and stimulus-evoked activity allows the separate characterization of attentional effects owing to modulation of the stimulus-evoked activity *per se*, or owing simply to changes in baseline activity independently of that evoked by the stimulus. Note that the requirement for a measure of stimulus-evoked activity independent of the attentional manipulation is largely a consequence of the time over which functional imaging measurements are acquired (of the order of seconds) relative to the time-scale over which the neuronal effects

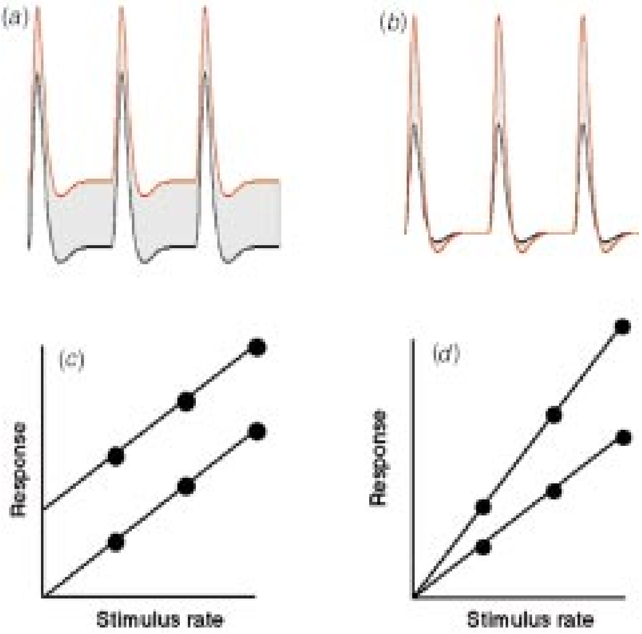

Figure 1. Theoretical illustration of bias and gain control mechanisms of attention. (*a*, *b*) Schematic illustration of how stimulus-evoked neural activity (red) might be modulated (grey) by an attentional signal. The form of this modulation could take the form of (*a*) an additive bias signal or (*b*) a true modulation of stimulus-evoked responses alone (*c*, *d*), varying the rate at which stimuli are presented produces a relation between the total evoked response (integrated over time) and the frequency of presentation. The attentional effects (*a*, *b*) can now be distinguished by their effects on intercept (*a*, *c*) or slope (*b*, *d*) of this relation, respectively.

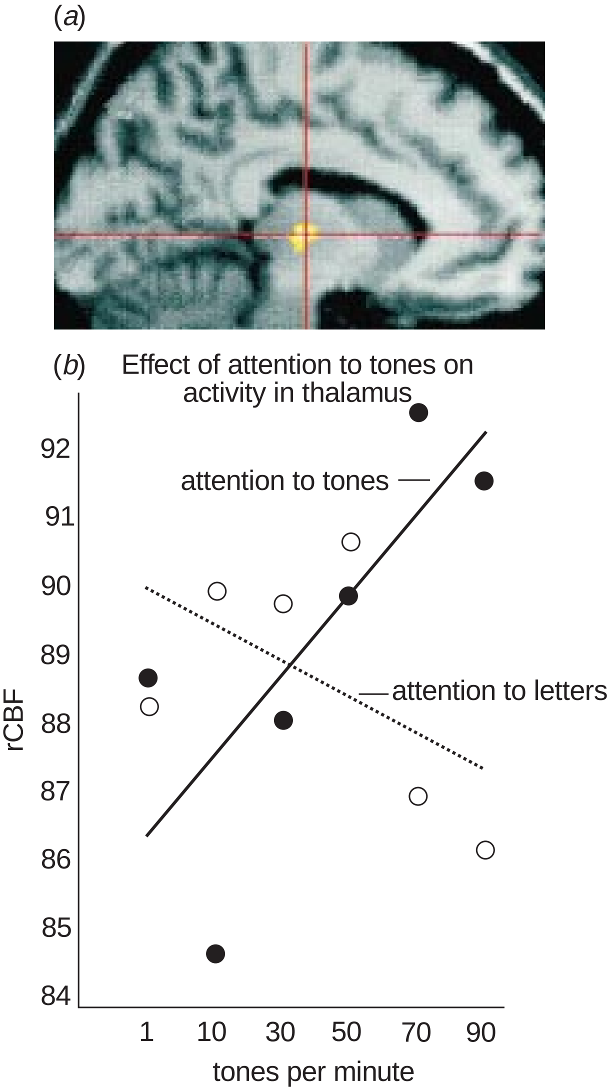

Figure 2. Modulation of thalamic rCBF by attention. (*a*) The area in the thalamus where attention to the auditory signals significantly modulates the correlation between cerebral blood flow and presentation rate is shown superimposed on a sagittal slice of the average structural MRI of the six subjects. (*b*) Cerebral blood flow in the thalamus plotted as a function of tone presentation rate for when subjects attend to the tones and when subjects attend to the visual signals.

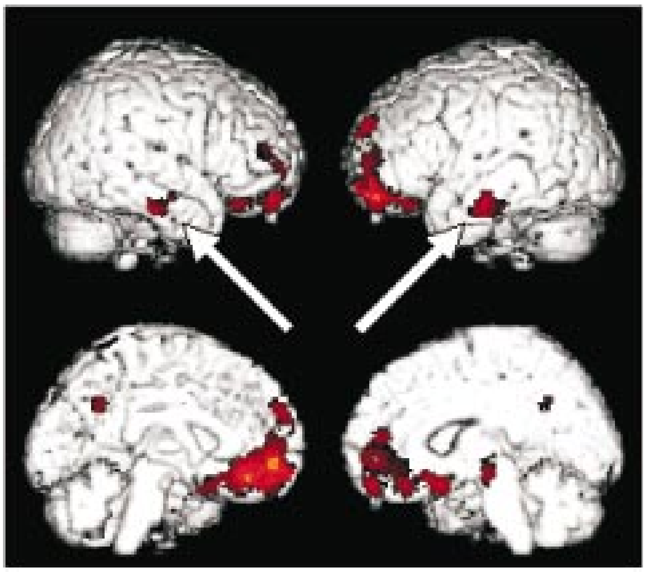

Figure 3. Decreases in cerebral blood flow correlated with rate. Areas that show significant decreases in regional cerebral blood flow with increasing stimulus presentation rate are rendered on a canonical T1-weighted structural MRI placed in the anatomical space of Talairach & Tournoux. The areas deactivated include medial frontal structures and bilateral areas of inferior temporal cortex (arrowed).

are manifest (of the order of milliseconds). This means that in any given trial, both stimulus-evoked activity and baseline activity are lumped together. To separate the effects of attention on each requires some independent manipulation of stimulus-evoked activity.

Frith & Friston (1996) proposed that such an independent measure of stimulus-evoked activity might be elicited by varying the rate of presentation of visual and auditory stimuli. The basis for this proposal is the observation that cerebral blood flow in primary sensory, primary motor and higher order association cortices increases with increasing stimulus presentation (Price *et al.* 1992; Frith & Friston 1996; Rees *et al.* 1997*c*; Sadato *et al.* 1997). The most likely interpretation of these results is that each stimulus produces a transient increase in blood flow such that the total increase in blood flow is directly related to the number of stimuli presented during the scan. This means that the slope of the line relating activity to presentation rate is an index of the amount of transient activity associated with the presentation of a single stimulus. Attention can now be investigated by studying how the slope or intercept of this line varies with the direction of attention (figure 1). A change in slope implies a true modulatory effect of attention; the amount of activity associated with each stimulus presentation is directly changed. On the other hand, a change in intercept implies that the activity associated with each stimulus presentation is unchanged, but instead a 'bias' signal, constant across different presentation rates, is added. This pattern implies that there may be activity in an area even in the absence of stimulus presentation.

The approach outlined here relies on measuring the relation between rCBF and a stimulus variable (presentation rate), and then examining how a manipulation of attention changes this relation. Certain assumptions are implicit in this approach that should be made clear. Most importantly, the assumption is made that within an area, the gain control or bias signal factor is constant across different presentation rates. If this assumption is incorrect then the measured changes in rCBF, although remaining a correct description of the effects of attention on rCBF, will be falsely attributed to a single underlying mechanism. In other words our approach makes the simplifying assumption of a unitary neurobiological mechanism of attention with a constant gain control or bias signal across the range of presentation rates studied. In our initial experiments a restricted range of presentation rates is used for this reason.

3. IMAGING THE MECHANISMS OF SELECTION

In this section we will review the three functional imaging experiments that have used a manipulation of stimulus presentation rate to characterize attentional effects. All have used positron emission tomography (PET), and this may be important as there is evidence that the functional magnetic resonance imaging (fMRI) signal dependency on rate of presentation of stimuli may be nonlinear, showing saturation as presentation rate increases (Binder *et al.* 1994; Rees *et al.* 1997*c*). These nonlinearities may be owing to stimulus habituation and would obscure or alter the interpretation of attentional effects in the approach we have outlined (Hillyard *et al.*, this issue). In the data presented here, obtained with PET, the relation between rCBF and presentation rate is linear throughout.

(a) *Does attention change the relation between rCBF and presentation rate?*

Frith & Friston (1996) correlated changes in cerebral blood flow with rate of presentation of simple tones to identify brain regions where auditory signals elicited a transient response. They compared one condition, where participants were asked to attend to the tones and ignore visual signals (single letters) presented at the same time, with another where participants were asked to attend to the visual signals and ignore the tones. They found that activity in the right thalamus was strongly correlated with the rate of presentation of the tones only when subjects attended to the auditory signals (figure 2). When attention was directed to the visual signals there was no correlation between cerebral blood flow and the presentation rate of the tones. In other words, the effect of attention in this area was to modulate the stimulus-evoked transient response produced by a single tone. Such an effect is similar to the conception of auditory attention as a 'gain control'. This experiment showed that PET is in principle able to detect one of the two types of attentional influence predicted on theoretical and empirical grounds here.

(b) *Can gain and bias effects of attention on cerebral blood flow be distinguished?*

The paradigm used by Frith & Friston (1996) used two very different streams of information and the items within stream to be monitored were highly distinguishable. Competition between stimuli would be expected to be minimal and, consistent with this, the participants found the task extremely easy. This study did not find any additive effects of attention on cerebral blood flow that would be consistent with a bias signal and it is possible that this was owing to the lack of competition between stimuli. We (Rees *et al.* 1997*a*) therefore extended this approach by using only a single visual stream, presented at a relatively fast rate and with unfamiliar abstract stimuli. Participants viewed a continuous stream of simple visual shapes (ellipses) that were oriented either horizontally or vertically and coloured red, green or blue. Participants were asked to attend to the visual stimuli and to classify them as targets or nontargets on the basis either of a single feature (for example, colour or orientation), or on the conjunction of features (colour and orientation together). We identified areas where there was a correlation between rate of presentation of the visual stimuli and cerebral blood flow, suggesting that task-related signals elicited a transient response in these areas. Several areas showed a positive correlation with rCBF, notably areas of extrastriate cortex and motor cortex contralateral to the hand that subjects used to make their responses. However, it was more interesting that several areas also showed a robust negative correlation with increasing presentation rate, including bilateral areas of inferior temporal cortex (figure 3). This pattern of changes in rCBF suggests that stimulus presentation is associated with a transient relative decrease in rCBF in inferior temporal cortex. The functional status of task-related decreases in haemodynamic activity has been controversial and often attributed to increases in cerebral blood flow in the control condition. The parametric design of this experiment, however, makes this explanation untenable and this pattern of blood flow changes suggests that regional decreases in rCBF may be functionally important. How might such changes in cerebral blood flow be reflected in underlying neuronal activity? The changes observed by using functional imaging techniques represent the overall rCBF response to changes in neural activity occurring in a population of several tens of thousands of neurons. The relation between reponses observed with single cell electrophysiology and changes in rCBF may therefore be complex, but our results limit the number of possible explanations. First, it could be that each stimulus evokes a transient decrease in overall neural activity in this area, accounting for the progressive fall in cerebral blood flow as presentation rate increases. However neurons in this area in monkey generally show increases in activity in response to stimulus presentation. An alternate possibility is that as rate increases, the amount of overall neural activity evoked by each stimulus becomes smaller or present for a shorter period of time. However, to give rise to a negative slope in the relation between rCBF and presentation rate, the magnitude of such a reduction would have to more than offset the increase in activity caused by merely increasing the presentation rate. Furthermore, such an effect must be caused by a neural mechanism specific to inferior temporal cortex, as other areas (for example, visual cortex) show increasing cerebral blood flow with increasing rate. This suggests that the decrease in cerebral blood flow in inferior temporal cortex is not caused by a general mechanism such as habituation of neuronal responses, but that there may be more specific mechanisms mediating such a decrease in activity.

Changes in cerebral blood flow owing to attending to conjunctions as opposed to features influenced the relation between rCBF and presentation rate in a number of areas. Activity in the left precuneus, premotor cortex and cerebellum showed an interaction effect, with a change in the slope of the line relating cerebral blood flow to presentation rate as a function of attention (figure 4). This type of effect is identical to the attention effect seen in the thalamus by Frith & Friston (1996). However, areas in the left inferior temporal cortex, and in the right cerebellar hemisphere showed an additive effect of attention with no change in the slope of the line relating rCBF to presentation rate. Taken together, these findings indicate that the operation of attention appears to result in two qualitatively different patterns of modulation of evoked haemodynamic activity, in keeping with

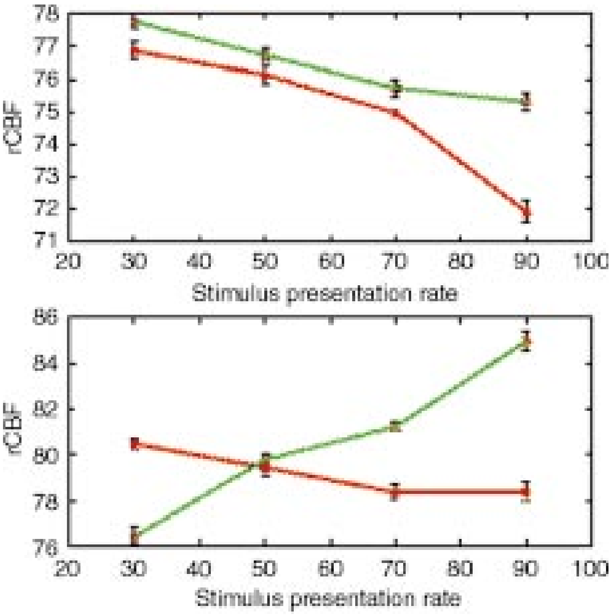

Figure 4. Two modulatory effects of attention on rCBF. (*a*) Cerebral blood flow in left inferotemporal cortex (see figure 3) plotted as a function of stimulus presentation rate, separately for attention to visual conjunctions (red line) compared with individual features (green line). There is a significant difference in the intercept of these two lines, but no significant difference in slope. This represents an additive effect of attention that is constant across presentation rates (cf. figure 1*a*). (*b*) Cerebral blood flow in the left premotor cortex plotted as a function of stimulus presentation rate, separately for attention to visual conjunctions (red line) compared with individual features (green line). There is a significant difference in the slope of these two lines. This effect represents an interaction between stimulus rate-evoked changes in rCBF and attention (cf. figure 1*b*).

our theoretical predictions. We will now discuss the effects of attention to conjunctions in inferior temporal cortex in more detail.

In one of the areas in inferior temporal cortex that showed a decrease in activity as presentation rate increased, there was a change in activity due to attending to conjunctions as opposed to features. The change in activity took the form of a decrease in activity in the conjunction task that was constant across all presentation rates (figure 4). This change in activity must be owing to the different attentional demands of the conjunction task, as the visual stimuli were the same across all tasks. In contrast to the attentional modulation seen by Frith & Friston (1996), this modulation takes the form of a baseline shift that is independent of the correlation of cerebral blood flow with stimulus presentation rate. In other words, the slope of the relation between cerebral blood flow and stimulus presentation rate is unchanged by attention, but the intercept is changed, consistent with a bias signal. The direction of the attentional effect is negative, decreasing evoked activity in inferior temporal cortex. We suggest two possible explanations for this type of effect. An explanation based on the feature integration theory (Treisman & Gelade 1980) would suggest that in the feature task, any relevant feature should trigger a correct response. However, in the conjunction task the separate features of the relevant conjunction will tend to evoke false alarms. They will therefore need to be inhibited, so that responses are made only to the correct conjunctions. In other words, more inhibition is required in the conjunction task giving rise to a lower overall evoked rCBF in inferior temporal cortex. An alternate explanation may be that conjunctions are coded in inferior temporal cortex as higher order combinations of single features. A hierarchical coding scheme would mean that fewer cells are selective for conjunctions compared with individual features. In such a scheme fewer cells would therefore need to be biased to give rise to selectivity for conjunctions as opposed to features. Overall neural activity evoked by feature selectivity would therefore be higher than for conjunctions, giving rise to a lower rCBF in the conjunction condition. Convergent functional imaging evidence supports the proposal that less activity is evoked in human inferotemporal cortex during the identification of conjunctions as opposed to individual visual features (Elliott & Dolan 1997). These authors showed a decrease in rCBF in left inferior temporal cortex when participants perform a visual delayed match to sample task on the basis of conjunctions of colour and form compared with individual features. The location of the area in left inferotemporal cortex identified by Elliott & Dolan (1997) is very close to that identified by Rees *et al.* (1997*a*), suggesting a common effect related to the identification of visual conjunctions of colour and form in both paradigms.

Relating the functional imaging findings in inferior temporal cortex to the neurophysiological data in monkeys is more difficult. Cells in inferotemporal cortex in monkeys show a range of different response properties. In delayed match-to-sample tasks, both cue-related activity in delay periods and enhanced responses to target stimuli matching a previous cue are seen. The presence of delay-related activity has been suggested as a neural correlate of an attentional bias signal (Desimone & Duncan 1995). Our functional imaging data is consistent with an additional signal associated with attention in inferior temporal cortex, independent of, and additive to, transient stimulus-evoked activity. However, whereas the activity of single cells shows an additive increase in activity, the functional imaging data shows an additive decrease in rCBF when conjunctions are compared with features. In other words, the response at the relatively coarse spatial scale detected by functional imaging is not the same as that recorded in a small number of single cells within this area. Intuitively this may seem plausible; for every cell that shows cue specificity and elevated delay-related activity within a single trial, most of the population will not show elevated delay-related activity. At a population level, the aggregate neuronal dynamics will therefore not necessarily bear a straightforward relation to the changes in firing rate of a single cell. Indeed, it is possible that although individual neurons show an increase in firing rate due to attention, the overall level of activity in a population of neurons may decrease if, for example, local interactions lead to suppression of activity. However, the relation of single cell activity to that of populations of cells in this area has not been explored experimentally in detail, so such a mechanism remains speculative.

(c) *How does attention modulate rCBF in visual and auditory cortex?*

The two previous experiments suggest that the effects of attention in human cortex are expressed in two different patterns of changes in cerebral blood flow. However, the modulatory effects that we observe are located relatively distant from extrastriate cortex, and may reflect the relatively abstract nature of the stimuli used. In the first experiment where there was relatively little competition between stimuli, only changes in stimulus-evoked activity were observed, whereas when there was more competition in the second experiment both changes in stimulus-evoked activity and changes compatible with a bias signal were seen. We therefore undertook a further experiment similar in conception to Frith & Friston (1996) in using both visual and auditory streams of information. However, to increase competition both within and between streams not only did presentation rate vary in both streams, but the stimuli and manipulations were the same in auditory and visual streams, decreasing their discriminability. In this study we attempted primarily to clarify the nature of attentional effects on extrastriate and auditory cortex. Participants were scanned while being presented with two concurrent streams of information, visual and auditory. They saw single letters presented at fixation, or single letters spoken binaurally through insert earphones. The letters varied both in their identity, and in their physical characteristics (grey-scale intensity or volume, respectively). In separate PET scans, participants were asked to attend either to the visual stream, or to the auditory stream and to press a button whenever a target appeared. In separate scans, the target was defined either on the basis of its identity or on its intensity (grey-scale or volume, depending on which stream was attended). We correlated changes in rCBF with changes in presentation rate of the targets, and studied how this relation changed in auditory and extrastriate cortex as a function of the direction of attention to visual or auditory streams. In both extrastriate and auditory cortex, directing attention to the appropriate modality produced a change in activity that was independent of the relation between stimulus presentation rate and cerebral blood flow (figure 5). In other words, the dominant attentional mechanism in both visual and auditory cortex in this study was an additive effect. This is not the only response property in extrastriate cortex, as a small area of right fusiform cortex showed an interaction between the attended modality and the relation between presentation rate and cerebral blood flow. Therefore it seems that, as already mentioned, PET is not in principle insensitive to changes in attention that directly modulate stimulus-evoked rCBF. Rather it seems that the dominant mechanism may be changes in rCBF in an area that are independent of, and additive to, stimulus-evoked rCBF.

The relation between these findings and the neurophysiological data concerning neural responses in monkey ventral stream processing is worth noting. Neurons in V4 and IT show changes in both stimulus-evoked activity and baseline firing rates as a function of attention. Changes in stimulus-evoked activity, if mirrored in changes in rCBF, would be expected to produce changes in the slope of the relation between rCBF and presentation rate. However, it seems that in the present study the dominant pattern of attentional modulation in extrastriate cortex takes the form of a change in the baseline activity, irrespective of presentation rate. There is therefore a discrepancy between the single cell and human data. The imaging experiments reviewed here suggest that PET is not in principle insensitive to the detection of attentional modulation of stimulus-evoked activity, so is it possible that a difference in paradigms may account for the discrepancy? In monkeys, attentional modulation of stimulus-evoked activity is seen only when both target and distractor are within a single receptive field. However, changes in baseline firing rates caused by attention are seen regardless of whether target and distractor are in the same receptive field, or presented sequentially at different times (Luck *et al.* 1997). Changes in the baseline firing rate may reflect a top-down signal that gives a competitive advantage to a stimulus at an attended location. This signal may bias one local population of cells over another, explaining why it is seen regardless of the positions of target and distractor within the receptive field (unlike the more local competition effects). The coexpression of stimulus-evoked and baseline shift activity within a single population of cells may explain the apparent discrepancy between single cell studies, where attentional effects are typically only seen when stimuli are placed within a single RF, and functional imaging studies. In such studies, including those reviewed here, stimuli have often been widely placed in locations expected to be in different receptive fields, or presented at different times. Over extended periods of time, with a relatively large interstimulus interval, changes in baseline firing rate might be expected to dominate the observed changes in rCBF. This explanation of the discrepancy is speculative, for there are many other respects in which functional imaging and electrophysiological paradigms are very different. However, our results presented here suggest that functional imaging techniques may be primarily sensitive to baseline shift activity. More closely analogous experiments done in both monkeys and humans may resolve this issue.

4. DISCUSSION

The data reviewed in § 3 show that two qualitatively different patterns of modulation of rCBF can be observed by using functional imaging techniques in experiments where non-spatial visual and auditory attention is manipulated. These patterns of modulation can be described as gain control and bias signal mechanisms. It is not yet clear whether these changes in cerebral blood flow can be directly identified with changes in baseline neural firing rates and modulation of stimulus-evoked activity by attention that have been observed in single neurons.

5. THE CONTROL OF ATTENTION

If regions of visual cortex show patterns of evoked neural and haemodynamic activity that can be interpreted as the effects of perceptual selection on stimulus-evoked activity, is it reasonable to seek evidence for structures involved in the control of attention? Some authors have argued that the multiplicity of definitions and dissociation of different types of behavioural effect due to attention makes the concept of a single attentional system untenable (Allport 1993). Nevertheless, considerable progress has been made in establishing the importance of parietal cortex in the shifting of spatial attention (see, for example, Corbetta *et al.* 1995). The experiments discussed in this paper all used non-spatial attentional tasks, where structures other than parietal cortex may be involved. Rees and co-workers (1997*a*) found that a single area of right prefrontal cortex, probably Brodmann area 8 (BA8), was activated by the conjunction task relative to the feature tasks. This area showed no correlation between stimulus presentation rate and cerebral blood flow, and so may be involved in establishing an attentional 'set', irrespective of rate and therefore independent of stimulus-evoked activity. This is compatible with the observation that ablation of this area in monkeys causes specific deficits in tasks involving a conjunction of visual and auditory inputs (Petrides & Iversen 1976, 1978). BA8 is well placed to be a source of modulatory influence, receiving connections from a wide range of cortical areas (Barbas & Mesulam 1985; Cavada & Goldman Rakic 1989). However, the homologies between monkeys and humans in this area of dorsolateral prefrontal cortex are not exact. For example, this area in monkeys contains the frontal eye fields, whereas in humans consistent functional imaging evidence suggests that the frontal eye fields are located in a more posteromedial location, in BA6 (Paus 1996). BA8 involvement in an attentional task was also shown by Rees & Frith in the experiment discussed in § 3c. Activity in right BA8 showed two different patterns. In one part of BA8, activity showed an interaction between the direction of attention to visual or auditory modalities, and the direction of attention within that modality (toward identity or intensity targets). Such a modulatory interaction would be expected if this area was involved in the control both of the between-modality direction of attention and the attentional 'set' within modality. In another part of BA8 that partly overlapped with the first area, evoked activity also showed a significant interaction between rate of presentation and the between-modality direction of attention. This is a surprising observation, as Rees and colleagues (1997*a*) found no effect of stimulus presentation rate in this area. However, the range of presentation rates used in this study was much greater than by Rees *et al.* (1997*a*) and the cerebral blood flow in this area depends not only on the presentation rate, but on the context of whether attention is directed to auditory or visual signals. Further studies will be needed to clarify the nature of presentation rate effects in both sensorimotor and 'attentional' areas of cortex. However the present results are consistent with a role for right prefrontal cortex in the direction of these attentional effects.

6. THE FATE OF REJECTED STIMULI

The discussion so far has considered the consequences for stimulus processing of choosing to attend to a particular stimulus attribute or part of the visual scene. The converse question can also be addressed by functional imaging experiments; namely, what is the fate of rejected stimuli? Behavioural research in this area has ranged widely over a variety of tasks in both auditory and visual modalities. In general, when subjects are asked to focus on certain stimuli and ignore others, it seems that only relatively large changes in the physical properties of the rejected stimuli result in spontaneous reports (Cherry 1957). However, in other circumstances it seems that the rejected stimuli can be extensively processed and influence behaviour as measured by indirect methods such as reaction time or evoked potentials (for a review, see Neill *et al.* 1995). It has not been clear why different paradigms produce such different results and there has been a long-standing debate about attention theory as to whether perception is dependent on attention (implying that ignored stimuli are not processed) or whether perception is independent of attention (implying that ignored stimuli are fully processed). Evidence from behavioural, electrophysiological and functional imaging experiments has been advanced to support one or other position, without consensus or resolution (Kahneman & Treisman 1984; Johnston & Dark 1986; Hillyard *et al.* 1987; Corbetta *et al.* 1991).

Lavie's theory (Lavie 1995) provides a theoretical resolution to this debate. She proposes that capacity for perception is limited, but within those limits perception proceeds automatically. So although limited capacity means that we cannot perceive everything, within those limits we are unable to stop perceiving whatever we can. The critical determinant of whether irrelevant stimuli can be ignored is therefore the degree to which the task we are engaged in exhausts available capacity. If the processing load of the task exhausts available capacity, irrelevant stimuli will not be perceived. However, if the target processing load is low, attention will inevitably spill over to the processing of irrelevant stimuli. In other words, we will only be successful in ignoring irrelevant stimuli if the task we are engaged in exhausts available capacity. This will occur only under conditions of high load. In her account, the selective nature of perception is contingent not simply on the existence of limited processing resources, but on the ability to allocate less than the available capacity if the task does not demand it. Note that the concept of processing load relates to increasing the number of items in a display, their similarity, or the degree of processing required for each item. This concept is related to the idea of competition elaborated by Desimone & Duncan (1995). However in Lavie's (1995) theory, it is different task requirements (high and low load) that produce differential competition for limited processing resources and hence differential processing of irrelevant stimuli.

A re-examination of the experimental data relating to the processing of irrelevant stimuli in the light of Lavie's theory is now possible (Lavie & Tsal 1994). Many of the tasks that show little evidence that irrelevant stimuli are processed are difficult, demanding tasks such as dichotic listening. In contrast, the behavioural evidence that irrelevant stimuli do indeed undergo processing is often gathered by using relatively austere paradigms with a limited number of items or low processing load. Furthermore, behavioural experiments specifically addressing Lavie's theoretical predictions show that irrelevant stimuli interfere more with behavioural responses under

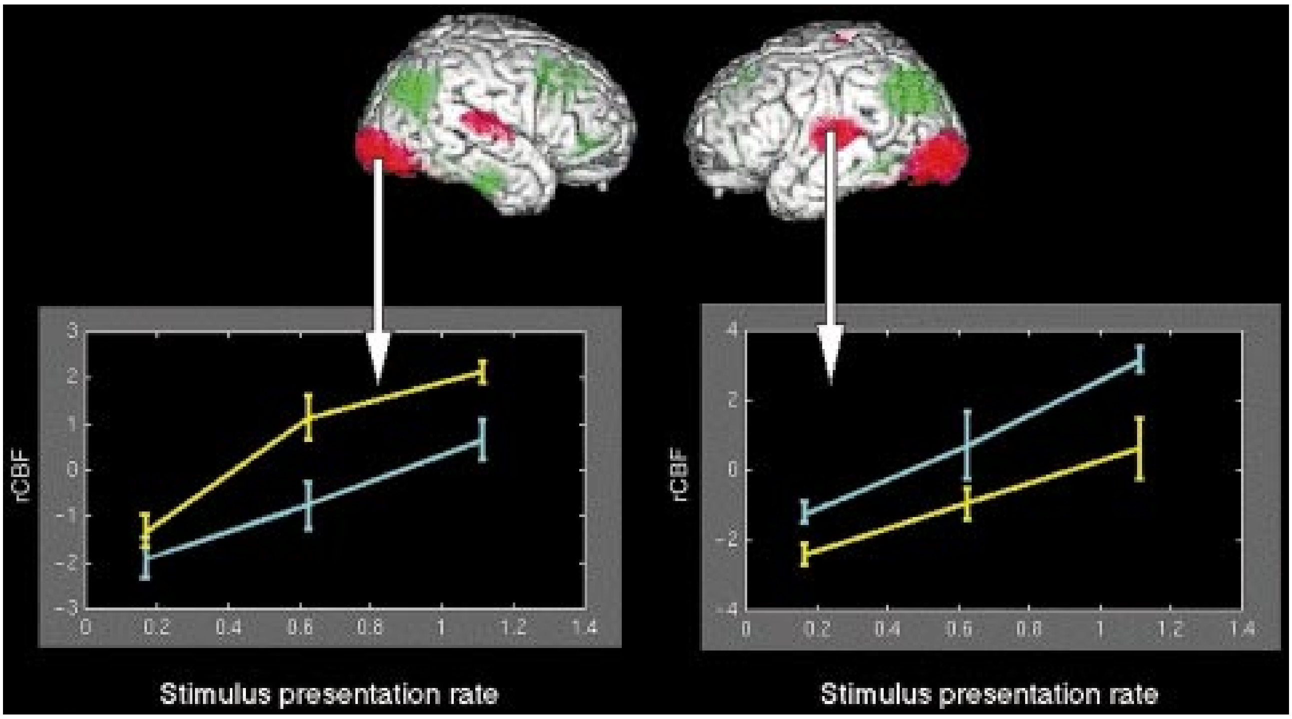

Figure 5. Right and left lateral views of areas where changes in cerebral blood flow show a significant positive (red areas) or negative (green areas) correlation with stimulus presentation rate. The activations are rendered on a canonical T1-weighted MRI image placed in the standard anatomical space of Talairach & Tournoux. Below visual (left) and auditory (right) cortex are plotted the relation between cerebral blood flow and stimulus presentation rate, as a function of attention to the visual signals (yellow line) or the auditory signals (blue line). In both cases there is an additive effect of attention, with no interaction between attention and stimulus presentation rate.

conditions of low load compared with high load conditions, suggesting a greater degree of processing (Lavie & Tsal 1994). The evidence therefore suggests that selective perception is dependent on attention only under conditions of high load.

7. IMAGING THE FATE OF REJECTED STIMULI

Investigating whether irrelevant stimuli are processed or not in a behavioural study requires an indirect measure of stimulus processing. Most often, this has been achieved by noting how indirect stimuli modulate or interfere with the primary task the subject is undertaking. Functional imaging offers the opportunity to circumvent the need for an indirect measure. fMRI allows non-invasive visualization of the evoked haemodynamics related to the processing of sensory signals (Kwong *et al.* 1992). If an irrelevant stimulus is known to activate a region of the brain functionally distinct from the areas activated by stimuli relevant to the task, then potentially this allows direct experimental observation of whether processing of the irrelevant stimuli has occurred. In the experiments reviewed here, there is some evidence to suggest that processing of irrelevant stimuli may occur. For example, Frith & Friston (1996) observed that there was a correlation between cerebral blood flow and the rate of presentation of tones in auditory cortex, even when subjects were attending to visual stimuli and attempting to ignore the auditory stimuli. Similarly in areas of extrastriate cortex, there is a correlation between letter presentation rate and cerebral blood flow even when subjects are attending to auditory information and ignoring the visual information. These observations suggest that processing of ignored auditory and visual stimuli may nevertheless take place under certain conditions. However, although these observations are suggestive, they fall short of a specific examination of the processing of irrelevant stimuli in the light of theories such as that of Lavie.

In collaboration with Lavie, we did a specific test of the predictions of her theory, that irrelevant stimuli are only processed under conditions of low load (Rees *et al.* 1997*b*). We used radial visual motion as an irrelevant stimulus. Visual motion is known to activate a functionally distinct cortical area, V5, whose location has been demonstrated in previous imaging studies (Zeki *et al.* 1991; Watson *et al.* 1993). Activation of V5 by moving as opposed to static irrelevant stimuli should allow us to determine whether processing of irrelevant motion has taken place. To modulate processing load, we used a linguistic task where subjects saw single words and monitored for the occurrence of targets. In both high and low load conditions, the subjects saw exactly the same physical stimuli, but the target criterion varied. Under low load conditions, targets were the words written in upper case letters; under high load conditions, targets were bisyllabic words. Activity evoked by the presence of irrelevant visual motion in the periphery of the display (compared with a static irrelevant stimulus) was significantly greater under conditions of low load (compared with high load) in several areas. In accordance with the predictions of Lavie's theory, an interaction between motion-related signals and perceptual load was seen bilaterally in V5 complex (see figure 6). Under conditions of low load, there was a significant activation in

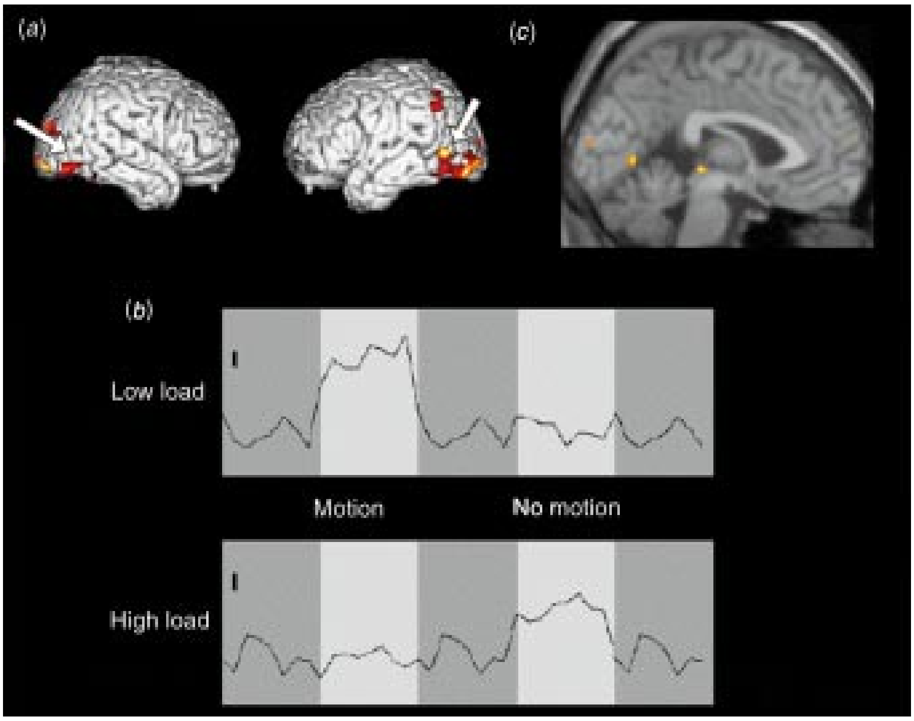

Figure 6. Modulation of ignored motion processing by attentional load. (*a*) Lateral views of the left hemisphere of a T1-weighted volume rendered anatomical image that conforms to the stereotactic space of Tailarach & Tournoux. On this image are superimposed in red the areas from where brain activity in the group of subjects showed the predicted interaction between the effects of visual motion and linguistic processing load. The locations of the left V5 complex is indicated by the arrows. (*b*) Mean activity over all subjects and replications of each experimental condition taken from the left V5 complex. Activity during baseline periods (dark grey shading) is shown alternating with that during experimental conditions (light grey shading). The scale bar represents a value of 0.1% BOLD signal change. (*c*) Activation in the superior colliculus produced by the interaction of motion processing and perceptual load, displayed on a sagittal slice from the same T1 canonical image as in *a*.

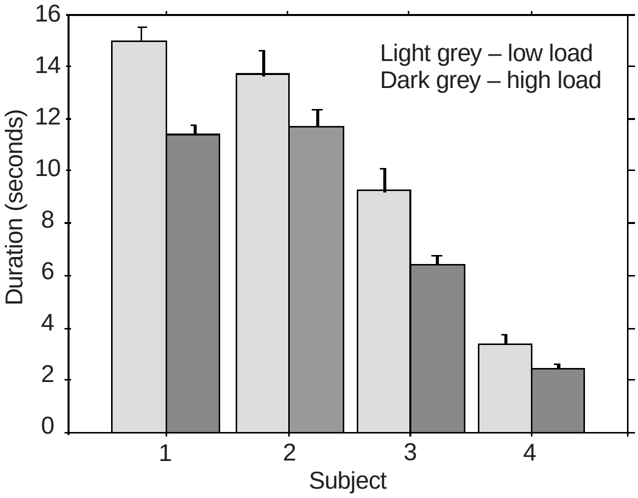

Figure 7. The mean duration of the motion after-effect for four subjects, measured after 32 s performing either low or high perceptual load tasks from the experiment described in the text. In each case there is a significant ($p < 0.05$, one-tailed) reduction in the motion after-effect under conditions of high perceptual load compared with low load.

these areas produced by moving dots; under conditions of high load the activation was reduced to baseline. In support of these results, a convergent behavioural experiment, modelled on those previously reported by Chaudhuri & Shulman (Chaudhuri 1991; Shulman 1991, 1993), showed that the motion after-effect (which is thought to be contingent on V5 activity (Tootell *et al.* 1996) was significantly shorter under conditions of high load (figure 7).

An interesting aspect of the findings of Rees and coworkers (1997*b*) is that a large number of areas outside V5 showed a modulation of motion-related signals by attentional load. In particular, areas very early in the anatomical hierarchy of visual processing, close to the V1–V2 border and in the superior colliculus (SC), showed such a pattern of modulation (figure 6). The involvement of the superior colliculus is particularly interesting in the light of an ablation study in monkeys (Desimone *et al.* 1990). Removal of the SC led to impairment in a visual discrimination task, but only under conditions where the unaffected part of the visual field contained a competing item. This suggests that the SC is sensitive to competition between stimuli. However, our results were obtained by manipulating the attentional load, rather than by changing the display in any way. Taken together, the work on monkeys and humans suggest that greater competition for attention may occur either as a consequence of increasing the number of visual items, or with more processing for the same items.

8. CONCLUSION

The experiments reviewed here suggest the feasibility of using functional imaging techniques to address directly the nature of the modulation of brain activity produced by attention. Variation of stimulus presentation rate provides a powerful way to characterize transient stimulus-evoked activity and to study the modulatory effects of attention. Such studies suggest that the effects of attention on rCBF are expressed in two different ways (bias and gain signals), and provide intriguing but incomplete parallels with single cell neurophysiological data. Further exploration of the assumptions underlying our approach and of the relation between changes in single cell activity and rCBF will enhance our understanding of these mechanisms. Finally, we have shown how specific cognitive theories about the operation of attention can be tested by using convergent fMRI and behavioural data, and demonstrated that stimuli that are ignored may nevertheless be perceived under certain circumstances.

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