

CHAPTER 20

**FEATURE- AND
OBJECT-BASED
ATTENTIONAL MODULATION
IN THE HUMAN
VISUAL SYSTEM**

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INTRODUCTION

THE human visual system has a limited processing capacity. Consequently, mechanisms of selective attention are needed to prioritize behaviourally relevant stimuli. Broadly speaking, the term ‘selective attention’ refers to a collection of mechanisms that insulate patterns of neural activity evoked by relevant stimuli from the deleterious effects of stochastic synaptic transmission and interference generated by other, irrelevant stimuli (Bisley and Goldberg 2003; Desimone and Duncan 1995; Mitchell, Sundberg, and Reynolds 2009; Moran and Desimone 1985; Pestilli, Carrasco, Heeger, and Gardner 2011; Reynolds and Desimone 1999; Reynolds, Pasternak, and Desimone 2000; Serences and Yantis 2006). Early studies of selective attention focused primarily on spatial attention, or selection that is based solely on a location that is likely to contain relevant information (e.g. Posner 1980). However, we often know the defining feature(s) of a stimulus (e.g. my keychain is red and rectangular) without knowing its specific location (e.g. my keys could be anywhere on the desk). Under these circumstances, relevant information may be selected in one of two ways: (1) on the basis of a single critical feature value (e.g. the colour red) or on the basis of a group of features bound into a holistic representation (e.g. a red rectangle). Here, we review behavioural and neurophysiological studies that examine the consequences and the sources of top-down feature- and object-based attentional control in the human visual system. While we also review a handful of

relevant single-unit recording studies in non-human primates, a thorough treatment of this literature can be found in Treue (chapter 21), this volume.

FEATURE-BASED ATTENTION

Behavioural evidence for feature-based attention

When scanning a crowded stadium to locate a friend, a successful search is facilitated by attending to a salient feature, like the colour of her baseball cap. Such anecdotal cases reveal a key property of feature-based attention (FBA): items throughout the visual field that contain the attended feature are prioritized while other features are muted (Egeth, Virzi, and Garbart 1984; Liu and Hou 2011; White and Carrasco 2011). For example, studies examining visual search performance suggest that observers can restrict search to only items that contain a target feature value while ignoring all others (Egeth et al. 1984; Treisman and Gelade 1980; Wolfe 1994; see also Wolfe (chapter 2), this volume). These findings prompted researchers to investigate how an attentional mechanism might act on the visual system in order to prioritize one feature over others. In an early study, Davis and Graham (1981) asked observers to report the presence of a grating in one of two sequential intervals. On 80–95% of all trials, the grating was rendered at a single spatial frequency (primary frequency). On the remaining trials the grating was rendered with a variable spatial frequency (secondary frequencies; randomly chosen from a set of six possibilities). As expected, observers detected the primary frequency with greater accuracy than any of the secondary frequencies. Moreover, detection rates generally declined as the size of the deviation between primary and secondary frequencies increased. Critically, the advantage for the primary frequency was eliminated when all frequencies were presented with equal probability. These findings suggest that observers can selectively monitor the responses of low-level feature-selective neuronal populations at the expense of others when it is behaviourally advantageous; several single-unit recording and human neuroimaging studies have corroborated this finding (Corbetta, Miezin, Dobmeyer, Shulman, and Petersen 1990, 1991; Ho et al. 2012; Liu, Larsson, and Carrasco 2007; Maunsell and Treue 2006; Scolari, Byers, and Serences 2012; Serences and Boynton 2007; Serences, Saproo, Scolari, Ho, and Muftuler 2009; Treue and Maunsell 1996; see ‘Neural evidence for feature-based attention’ below).

Several researchers have argued that space-based attention (SBA) increases the effective salience of a stimulus akin to a change in local contrast, and this may be true for FBA as well (Carrasco 2011; Carrasco, Ling, and Read 2004). Support for this view has been reported in adaptation studies, where prolonged exposure to a feature or object leads to a potent after-effect. In one example, Lankheet and Verstraten (1995) measured the relative strength of motion after-effects (MAE; the tendency to perceive motion with a trajectory opposite to that of a physical stimulus after prolonged viewing) induced by

attended and unattended motion dot fields (kinetograms). During the adaptation phase, subjects were instructed to attend one of two spatially superimposed kinetograms that moved in opposite directions. Following adaptation, subjects performed a discrimination task where they were required to report the direction of a test stimulus that contained some proportion (0–100%) of coherently moving dots. The logic of this approach was as follows: selectively attending to one kinetogram during the adaptation phase of the experiment should enhance its salience relative to the unattended kinetogram and lead to a stronger MAE. Consequently, when presented with a test stimulus moving in the same direction as the attended dot field (and opposite in direction relative to the MAE), observers would require relatively high levels of motion coherence in order to perform the discrimination task with criterion accuracy (compared to trials without prior adaptation). This is precisely what the authors found: despite equivalent sensory stimulation, the strength of adaptation was greater for the attended relative to the unattended kinetogram. This result is consistent with the hypothesis that FBA increases the effective saliency of an attended stimulus.

In a subsequent study, Rossi and Paradiso (1995) asked subjects to discriminate either the orientations or spatial frequencies of two sequentially presented foveal gratings (primary task). On one third of trials, subjects were also prompted to report the presence or absence of a near-threshold peripheral grating (secondary task; see Fig. 20.1a). The spatial frequency and orientation of the peripheral grating sometimes matched (1/5 of target present trials) and sometimes mismatched the features of the foveal stimulus. Note, however, that the features of the peripheral grating were task-irrelevant. Nonetheless, when subjects attended to orientation in the primary task, they detected peripheral gratings at matched orientations (0° for the results depicted in Fig. 20.1b) with higher accuracy than those at mismatched orientations. Conversely, detection performance did not differ across spatial frequencies (i.e. the unattended feature; the matched spatial frequency is 0.5 cycles per degree, or cpd, for the results depicted in Fig. 20.1b). Importantly, these effects disappeared when subjects were not required to attend the central stimulus, suggesting that the advantage for matching peripheral stimuli was not simply a passive sensory effect. These results suggest that feature-based selection facilitates the processing of attended feature values across the entire visual field, and subsequent psychophysical evidence has corroborated this finding (Arman, Ciaramitaro, and Boynton 2006; Liu and Hou 2011; Sàenz, Buračas, and Boynton 2003; White and Carrasco 2011; see also ‘Neural evidence for feature-based attention’ below).

While FBA can be deployed across all of visual space, many studies have shown that it may also be restricted to only certain features of an object. For example, under certain circumstances attention may select task-relevant features without also selecting irrelevant ones belonging to the same stimulus (Corbetta et al. 1991; Lu and Itti 2005; Rossi and Paradiso 1995). This is illustrated in the Rossi and Paradiso (1995) study described above: the detection results indicated that while subjects attended to only the orientation of the primary grating, they ignored spatial frequency (the behaviourally irrelevant feature). However, one must be careful not to overgeneralize this result,

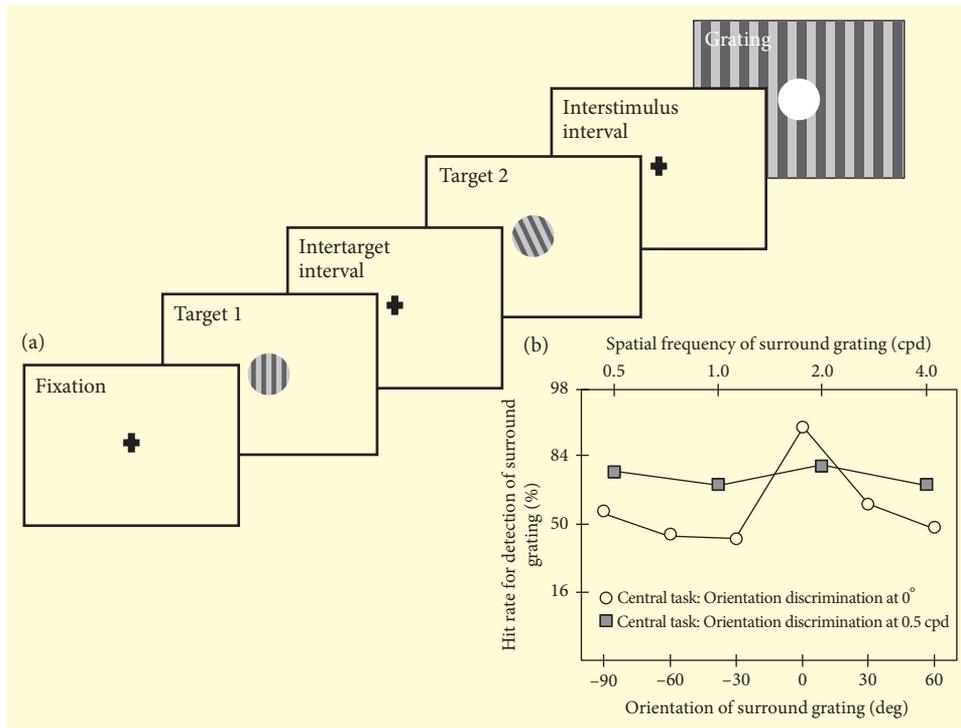


FIGURE 20.1 (a) Schematic representation of the task used in Rossi and Paradiso (1995). Subjects first completed an orientation discrimination task, in which they reported the directional rotation of a second Gabor patch (target 2) relative to the first Gabor patch (target 1). On a random one third of trials, subjects were instructed also to report the presence or absence of a secondary peripheral grating (shown here); it was present on one sixth of all trials and either matched or mismatched the orientation and spatial frequency of target 1. Note that while this illustration is made up of square-wave gratings, the actual experiment utilized sinusoidal waves. (b) Depiction of a single subject's results for the secondary orientation detection task (open circles) and secondary spatial frequency detection task (filled squares) when the subject was attending to orientation in the primary discrimination task.

as other studies have reported enhanced processing of task-irrelevant features paired with a target feature (Arman et al. 2006; Melcher, Papathomas, and Vidnyánszky 2005; Sohn, Chong, Papathomas, and Vidnyánszky 2005), even outside the locus of SBA. In one example (Sohn et al. 2005), subjects were instructed to attend one of two spatially superimposed random dot kinetograms (differentiated by colour) rendered in one visual hemifield ('attended hemifield') in order to detect changes in luminance. Two task-irrelevant spatially superimposed kinetograms were also rendered in the opposite hemifield ('unattended hemifield'), one of which moved in a single direction with 100% coherence. Subjects experienced significantly longer MAE durations when the colour of the high-coherence task-irrelevant kinetogram matched the colour of the attended random dot pattern than when it did not, even though motion was irrelevant to the

task. Furthermore, in a similar version of the study adapted for functional magnetic resonance imaging (fMRI), the magnitude of the blood-oxygenation-level-dependent (BOLD) response in MT+ to the task-irrelevant kinetogram was significantly stronger when it shared the target's colour. It should also be noted that some feature-based attentional spreading was similarly evident in the Rossi and Paradiso (1995) study: when subjects attended to the spatial frequency of the central Gabor patch, detection performance for peripheral gratings revealed feature selectivity for both spatial frequency and orientation (though note that this effect was asymmetrical, as similar spreading did not occur while subjects attended orientation).

In a subsequent study, Lu and Itti (2005) measured the relative perceptual benefit afforded to a secondary stimulus when it shared task-relevant and/or task-irrelevant features with a behaviourally prioritized primary stimulus. A shared irrelevant feature across stimuli provided no additional perceptual benefit to the secondary stimulus if the relevant feature was also shared. Conversely, a small benefit was observed when the secondary stimulus shared only a task-irrelevant feature with the primary stimulus, relative to a condition where no features were shared. Based on these results, Lu and Itti argued that paired irrelevant features are only weakly enhanced compared to relevant features. Thus, at present, the boundary conditions determining when attention can be restricted to a subset of features within an object are unclear. We revisit this issue under 'Object-Based Attention,' below.

Neural evidence for feature-based attention

Psychophysical demonstrations like those described in the preceding section can point to possible mechanisms of FBA, but they cannot unambiguously reveal how underlying changes in brain activity lead to the observed behavioural effects. Early demonstrations of FBA effects in the visual system primarily came from single-unit recording studies with rhesus monkeys (Haenny and Schiller 1988; Spitzer, Desimone, and Moran 1988). For instance, Haenny and Schiller (1988) documented FBA effects in visual cortex while a monkey attended to a precued orientation. Attentional modulation was observed in V₄ and to a lesser extent V₁, both of which contain neurons that are selective for orientation. Subsequent single-unit recordings have demonstrated similar modulatory patterns across the visual hierarchy (reviewed by Boynton 2005; Maunsell and Treue 2006; Serences and Yantis 2006). Given the strength of modulation observed in early visual areas, one of the first human neuroimaging studies of FBA targeted regions according to their presumed sensory selectivity (Corbetta et al. 1990, 1991). These positron emission topography (PET) studies revealed that attending to the shape, colour, or velocity of a set of objects during a difficult discrimination task differentially activated corresponding human extrastriate visual areas selective for these features.

In the previous section, we discussed psychophysical evidence to suggest that FBA is deployed across the entire visual field, regardless of target location (Rossi and Paradiso 1995). Evidence from human neuroimaging across visual areas motivates a similar

conclusion (Liu, Larsson, and Carrasco 2007; Serences and Boynton 2007). For example, Sàenz, Buračas, and Boynton (2002) instructed observers to attend to one of two overlapping dot fields of upward and downward motion respectively, while an ignored dot field on the opposite side of space moved either upward or downward. Consistent with previous findings that support a spatially global recruitment account of FBA (e.g. Rossi and Paradiso 1995; Treue and Martinez-Trujillo 1999), the BOLD responses to the ignored dot field were modulated in accord with the attended dot pattern in the opposite visual field for all tested regions (V_1 – V_3A and $MT+$). A similar result was observed for colour when subjects attended to either red or green dots. Moreover, subsequent work has demonstrated that cortical areas that were not directly driven by a stimulus also exhibited selectivity for an attended feature (Serences and Boynton 2007; see Fig. 20.2), suggesting that FBA modulates the firing rates of neurons tuned to the relevant feature irrespective of their spatial receptive field (Andersen, Fuchs, and Müller 2009; Liu and Hou 2011; Sàenz et al. 2003; Serences et al. 2009; White and Carrasco 2011).

In a recent study, Schoenfeld et al. (2007) obtained fMRI, electroencephalographic (EEG), and magnetoencephalographic (MEG) measurements while subjects performed a demanding motion or colour discrimination task. This approach allowed the authors

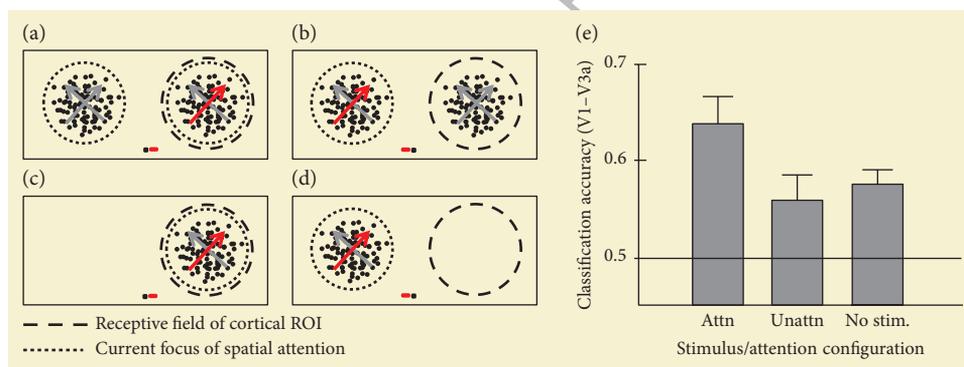


FIGURE 20.2 Adapted from *Neuron*, 55 (2), John T. Serences and Geoffrey M. Boynton, Feature-Based Attentional Modulations in the Absence of Direct Visual Stimulation, pp. 301–12, Copyright (2007), with permission from Elsevier. In this neuroimaging study, subjects attended one of two superimposed kinetograms to detect brief perturbations in speed. A central cue signals the location and direction of motion of the relevant stimulus (as depicted here, the red line at fixation indicates that subjects attend the 45° kinetogram and ignore the 135° one). (a–d.) A depiction of the different possible stimulus configurations, with respect to a cortical region of interest (ROI) under consideration; in these depicted cases, the ROI always receives input from the right visual field (as indicated by the thick dotted line). (a) Spatial attention is directed inside the receptive field (RF) of the ROI, and a second set of kinetograms is presented in the ignored hemifield. (b) Spatial attention is directed away from the RF of the ROI, which is stimulated by a set of ignored kinetograms. (c) Spatial attention is directed inside the RF of the ROI, and the ignored hemifield is empty. (d) Spatial attention is directed away from the RF of the ROI, which is not stimulated. (e) Depiction of classification accuracy for attended motion direction, averaged across V_1 – V_3a , for an attended ROI, an unattended ROI, and an unstimulated ROI.

to (1) verify visual cortical areas whose responses are modulated by FBA (e.g. by identifying regions that show a greater fMRI BOLD response when attention is directed to a single feature), and (2) examine the time course of these attentional effects (by examining changes in the amplitudes of EEG and MEG responses time-locked to the onset of the stimulus array). As in earlier neuroimaging work (e.g. Sàenz et al. 2002), Schoenfeld et al. reported that directing attention to either the motion or colour of a moving dot kinetogram selectively enhanced the amplitude of the fMRI BOLD response in visual cortical areas hMT+ and V4, respectively. Concurrent EEG and MEG recordings revealed that the attention-related response enhancement in these specialized cortical areas began as early as 90–120 ms following stimulus onset. This ‘between-feature’ selection—in which attention is directed to one of two orthogonal feature dimensions—occurred in an earlier epoch than previous observations of feature selection among values within a shared dimension (‘within-feature’ selection; e.g. Anllo-Vento, Luck, and Hillyard 1998; Liu, Stevens, and Carrasco 2007). This prompted Schoenfeld et al. to conclude that feature selection *between* dimensions is faster than feature selection *within* a dimension. However, Zhang and Luck (2009) demonstrated that at least under some conditions, within-dimension selection can also operate very rapidly following stimulus onset.

Given that FBA can modulate neuronal responses very quickly following stimulus onset, Schneider (2011) hypothesized that it might also manifest at subcortical levels, analogous to spatial attention. Previous studies indicate that retinotopically organized subcortical regions, such as the lateral geniculate nucleus (LGN) and pulvinar, exhibit feature selectivity (Ferster, Chung, and Wheat 1996; Merigan and Maunsell 1993; Petersen, Robinson, and Keys 1985; Wiesel and Hubel 1966). Schneider (2011) therefore measured FBA effects using high-resolution fMRI at these subcortical levels while subjects detected changes in either the colour (coded by the parvocellular layers of the LGN) or motion (coded by the pulvinar and magnocellular layers of the LGN) of one of two superimposed kinetograms. As expected, the BOLD responses were substantially greater in each region of interest (ROI) when the preferred feature was attended. This suggests that top-down attention operates at multiple levels along the visual hierarchy, including anatomically early regions in the thalamus.

Models of feature-based attention

Single-unit recording studies suggest that FBA enhances the firing rate of neurons that are selectively tuned to a behaviourally relevant feature, regardless of the locus of spatial attention (Treue and Martinez-Trujillo 2007; Treue and Martinez-Trujillo 1999). This modulation is thought to amplify responses associated with the attended feature and to attenuate responses associated with the irrelevant feature(s), thus enhancing the separability of the relevant representation from those of competing distractors. These hypotheses are codified in the feature similarity gain model developed by Treue and Martinez-Trujillo (Martinez-Trujillo and Treue 2004; Maunsell and Treue 2006; Treue and Martinez-Trujillo 1999). This account holds that attention modulates all

sensory neurons that are tuned along the relevant feature dimension: the level of gain afforded each unit is proportional to its response to the attended feature. This means that maximally driven neurons are enhanced the most (see Fig. 20.3a; Martinez-Trujillo and Treue 2004; Maunsell and Treue 2006; McAdams and Maunsell 1999; Treue and Martinez-Trujillo 1999), while neurons tuned to opposing, irrelevant feature values are suppressed. This mixture of excitation and inhibition effectively ‘sharpens’ the population response to the attended feature, which presumably then facilitates the detection and discrimination of relevant features.

The feature similarity gain model has had an enormous influence on investigations of FBA (Carrasco 2011). In general, this model provides a good description of data obtained in tasks where subjects are required to make coarse discriminations (e.g. between two orthogonal directions of motion). From a computational perspective, enhancing the gain of the maximally responsive (on-channel) neurons is optimal for discriminating between dissimilar stimuli: the Gaussian-shaped neuronal tuning function peaks at the target orientation while the distractor orientation falls at a local minimum, therefore resulting in the highest signal-to-noise ratio (SNR). However, given the response properties of sensory neurons, two similar orientations (e.g. 90° and 92° ; fine discrimination) will elicit similar firing rates from neurons tuned to either orientation (Hol and Treue 2001; Navalpakkam and Itti 2007; Regan and Beverley 1985; Seung and Sompolinsky 1993). This means that applying gain to the neurons tuned to the target feature will not result in much change in the SNR, and will thus likely provide little information in a discrimination task. Recently, models of FBA have incorporated this logic to suggest that attentional gain should be applied to neurons tuned to a flanking (off-channel) orientation during fine discriminations (Navalpakkam and Itti 2007),

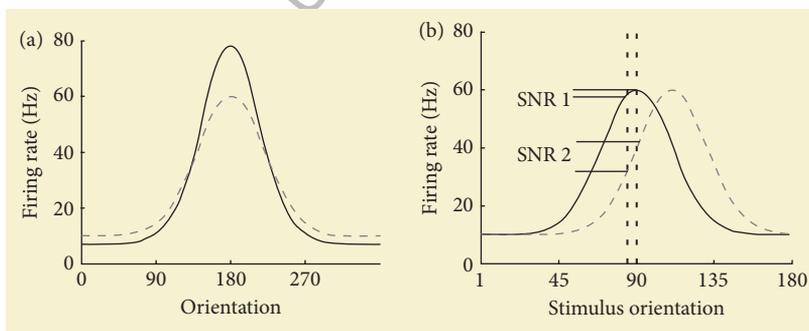


FIGURE 20.3 (a) Illustrations of hypothetical tuning functions for an orientation-selective sensory neuron with a preference for 180° in the absence of attention (dotted line) and when the neuron's preferred orientation is attended (solid line). Here, feature-based attention enhances the response of the maximally responsive neuron as described by the feature similarity gain model. Figure adapted from Boynton (2005). (b) Alternatively, as indicated by optimal gain models, off-channel sensory neurons that flank the behaviourally relevant feature are most informative during a fine discrimination because they yield a relatively high signal-to-noise ratio (SNR) compared to on-channel neurons. Target (90°) and distractor (92°) orientations are marked by vertical dashed lines. Adapted from *Neuron*, 53 (4), Vidhya Navalpakkam and Laurent Itti, Search Goal Tunes Visual Features Optimally, pp. 605–17, Copyright (2007), with permission from Elsevier.

where the firing rate differences between stimuli will be maximized (therefore resulting in a high SNR; see Fig. 20.3b). Scolari and Serences (2009) provided psychophysical evidence suggesting that humans can deploy FBA in this off-channel manner during a difficult fine discrimination, and that such modulation in primary visual cortex aids in decision-making (Scolari et al. 2012; Scolari and Serences 2010). Furthermore, relative off-channel gain predicted behavioural performance, on a between- (Scolari and Serences 2009) and within-subject basis (Scolari et al. 2012; Scolari and Serences 2010). Based on these findings, we suggest that feature-based attentional gain can be deployed in a flexible manner across populations of low-level sensory neurons depending on the nature of the task. Thus, a modification to the feature similarity gain model may be in order that takes into account the current goals of the observer: rather than stipulating that gain is applied to sensory neurons in proportion to the similarity between tuning preference and target, the model may instead stipulate that attentional gain is applied in proportion to the informativeness of sensory neurons.

Efficient selection: Feature-based attention

The goal of FBA, as alluded to throughout this chapter, is to prioritize behaviourally relevant information so that it may be properly utilized in the decision-making process. Indeed, many studies reviewed here have demonstrated that FBA improves performance on a range of perceptual tasks (e.g. Rossi and Paradiso 1995; Sàenz et al. 2003; White and Carrasco 2011). Given the strong evidence that FBA operates at the level of sensory coding, it is also worthwhile to explore how FBA influences decision-making mechanisms. For instance, visual information that is coded in low-level areas must be fed forward to later decision-making regions (e.g. lateral intraparietal area (LIP), dorsal-lateral prefrontal cortex (DLPFC), frontal eye field (FEF), etc.; Gold and Shadlen 2001, 2003, 2007; Hanes and Schall 1996; Horwitz, Batista, and Newsome 2004; Leon and Shadlen 1999; Roitman and Shadlen 2002; Schall 2001; Shadlen and Newsome 2001) and the efficiency of this ‘read-out’ process will influence the speed and accuracy of perceptual decisions (Das, Giesbrecht, and Eckstein 2010; Palmer, Huk, and Shadlen 2005).

In the preceding section, we discussed how FBA can flexibly modulate the firing rates of the most informative sensory neurons given a specific behavioural task (Navalpakkam and Itti 2007; Scolari et al. 2012; Scolari and Serences 2009). This information could be further amplified by preferentially weighting informative sensory signals during decision-making, which could operate either in lieu of, or concurrently with, sensory gain. For example, during a fine-motion discrimination task, MT neurons tuned to directions of motion that flank the target are found to be the most informative (Jazayeri and Movshon 2006, 2007), and simulations of fine-motion discriminations revealed that these off-channel MT-like neurons (tuned to directions of motion offset from a target direction by $\sim\pm 40^\circ$ in this case) may be weighted most strongly by LIP neurons during decision-making (Law and Gold

2008, 2009; Purushothaman and Bradley 2005). Notably, this type of reweighting by later decision mechanisms may account for improved perceptual performance, independent from any changes in sensory gain.

Pestilli et al. (2011) jointly modelled psychophysical and BOLD data to determine how changes in sensory gain, noise reduction, and/or efficient ‘read-out’ of information could account for changes in contrast detection thresholds. Although the authors observed an additive shift in the BOLD signal measured from visual cortex (V_1 – hV_4) on trials in which a target location was precued (focused attention trials) relative to trials in which all locations were precued (distributed attention trials), this response enhancement could not adequately account for corresponding changes in behavioural performance between conditions; nor could an additional reduction in the variability of the BOLD response. The data instead were best fit by a model that included both additive response changes in early visual areas coupled with a selective read-out rule in which inputs from the most responsive neurons are preferentially weighted by decision mechanisms. Thus, the biased read-out rule effectively amplified the impact of the small additive increase in the evoked BOLD response. While this study focused only on SBA, it is conceivable that similar selective pooling rules may apply to FBA as well. However, future research is required to explore the impact of biased sensory read-out rules, particularly as FBA studies continue to reveal a dynamic, sophisticated system that operates in accordance with behavioural goals.

Control of feature-based attention

While much of the FBA literature has focused extensively on feature-based attentional modulation in visual cortex, recent work has begun to explore where and how top-down control signals might instantiate and mediate these effects. For example, shifts of spatial attention appear to be guided by a distributed frontoparietal network that includes superior parietal lobule (SPL), intraparietal sulcus (IPS), FEF, and supplementary eye field (SEF; Corbetta and Shulman 2002; Kastner and Ungerleider 2000; Szczepanski, Konen, and Kastner 2010; Yantis et al. 2002), and there is some evidence suggesting that shifts of FBA might be mediated by a similar network (Corbetta and Shulman 2002; Greenberg, Esterman, Wilson, Serences, and Yantis 2010; Le, Pardo, and Hu 1998; Liu, Hospadaruk, Zhu, and Gardner 2011; Liu, Slotnick, Serences, and Yantis 2003; Pollmann, Weidner, Müller, and Cramon 2000; Rushworth, Paus, and Sipila 2001). For example, Liu et al. (2003) asked subjects to attend the colour or direction of a dynamic kinetogram that changed colours and directions multiple times during the course of a trial. Certain feature values (e.g. the colour red or upward motion) directed subjects to switch attention from one feature dimension to another (‘switch’ cues), while others (e.g. green or leftward motion) directed subjects to hold attention on the current feature dimension (‘hold’ cues). Using fMRI, Liu et al. were able to identify cortical areas that showed stronger responses following ‘switch’ relative to ‘hold’ targets, including left precentral gyrus, precuneus, and left IPS. These areas may be involved in attentional

control across different mechanisms, as similar patterns of switch-related activity have also been observed when subjects shifted between spatial locations (Yantis et al. 2002), objects (Serences, Schwarzbach, Courtney, Golay, and Yantis 2004), and even modalities (e.g. vision vs audition; Shomstein and Yantis 2004b, 2006).

Greenberg et al. (2010) similarly found a common BOLD signal corresponding to both space-based and feature-based shifts of attention in posterior parietal cortex and prefrontal cortex, including medial SPL, FEF, SEF, and left medial frontal gyrus, while subjects shifted attention either between or within locations and colours. Domain-general attentional control centres in frontal and parietal cortex have also been implicated in other studies (Liu et al. 2011; Liu et al. 2003; Shomstein and Yantis 2004b). In particular, converging evidence from both fMRI and transcranial magnetic stimulation (TMS) studies has added further support to the domain-general role subregions of the parietal lobe play in shifting of attention: Schenkluhn, Ruff, Heinen, and Chambers (2008) reported that stimulating anterior IPS disrupted both spatial and feature-based selection mechanisms (consistent with Wojciulik and Kanwisher 1999), while stimulation to the supramarginal gyrus only disrupted SBA. How the same network controls the selection of multiple features as well as locations within sensory cortex, and how such control may be exerted differently depending on task demands, however, warrants further exploration. One possibility is that subunits within these areas play different roles in mediating each type of control (Greenberg et al. 2010; Liu et al. 2011; Yantis and Serences 2003). For example, Greenberg et al. (2010) demonstrated that patterns of activation within medial SPL could be used to accurately classify attentional shifts between locations and attentional shifts between colours, suggesting that interdigitated populations of cells in SPL may control different forms of selection. Liu and colleagues also found differential patterns of activation in topographically defined IPS (IPS₁₋₄) when subjects attended to either colour or motion, as well as in FEF, suggesting that different features may recruit distinct subpopulations in a frontoparietal network.

OBJECT-BASED ATTENTION

In the previous section, we described how humans can select relevant information on the basis of simple feature values (e.g. a particular colour). However, objects in a visual scene consist of many features, all or part of which may be behaviourally relevant. Although converging evidence from the FBA literature reveals that relevant features within an object are afforded a representational bias, other studies have shown that selective attention can extend to all features in an object. Below, we review behavioural and neural evidence suggesting that attention sometimes operates in an *object-based* manner by simultaneously enhancing the cortical representations of all features within a selected item, even when some of these elements are wholly task-irrelevant. This selection can occur either when all features of a complex object are simultaneously enhanced,

or when the boundaries of an object constrain the spread of SBA. We discuss how behavioural goals and task demands might explain why FBA is observed in some cases, while OBA is observed in others.

Behavioural evidence for object-based attention

It is well known that attention can be used to select behaviourally relevant complex objects at the expense of others, even if those objects appear with overlapping distractors (Scholl 2001). In one early demonstration, Neisser and Becklen (1975) instructed subjects to attend to the events depicted in one of two superimposed videos. While subjects focused on one video, unusual events occurring in the unattended video were often missed (see also Simons and Chabris 1999). Given that most objects in the videos occupied the same spatial locations, these findings are most parsimoniously explained by a selection mechanism that operates on object representations rather than spatial positions.

Duncan (1984) later reported more direct evidence for the existence of an object-based selection mechanism. He showed subjects brief displays containing a spatially superimposed box and line and asked them to report either one dimension of a single object (e.g. the size of the box), two dimensions of a single object (e.g. the size of the box and the location of a small gap on its contours), or one dimension from each of the two objects (e.g. the size of the box and the tilt of the line). Subjects were equally good at reporting one or two dimensions of a single object, but task performance declined precipitously when subjects were required to report one attribute from each of the two objects. Subsequent studies have replicated this basic pattern using an impressively diverse array of stimuli and behavioural paradigms (Baylis and Driver 1993; Behrmann, Zemel, and Mozer 1998; He and Nakayama 1995; Kramer and Jacobson 1991; Melcher et al. 2005; Mitchell, Stoner, and Reynolds 2004; Sohn, Papatthomas, Blaser, and Vidnyánszky 2004; Valdes-Sosa, Cobo, and Pinilla 2000). Critically, these findings cannot be readily explained by classic models of SBA as all stimuli were spatially superimposed and thus could not be selected purely on the basis of their location. Instead, together they point to the existence of an attentional mechanism that prioritizes whole objects.

Evidence for OBA has also been reported in cueing tasks that are typically used to study spatial selection (Egly, Driver, and Rafal 1994; Moore, Yantis, and Vaughan 1998). In one example, Egly et al. (1994) presented subjects with displays containing two parallel rectangles arranged above and below or to the left and right of fixation (see Fig. 20.4a). On each trial, a target item appeared at one corner of one rectangle, and subjects were asked to report its location as quickly as possible. Shortly before target onset, an exogenous precue was flashed at one corner of one rectangle. On 75% of trials, the cue appeared at the same location as the upcoming target ('valid' trials), and on the remaining 25% of trials, the cue appeared at a non-target location ('invalid' trials). Critically, two types of invalid trials were possible: (1) the cue could appear on

the opposite end of the same rectangle as the upcoming target ('same-object' cues); or (2) the cue could appear on one end of the other rectangle ('different-object' cues). As expected from previous SBA studies, subjects' responses were significantly slower on invalid relative to valid trials. However, this effect was larger for different-object relative to same-object cues, even though same- and different-object cues appeared at the same absolute distance from the target (see Fig. 20.4b). This result implies a processing advantage for items that appear within the same structured space as an attended location.

One explanation for the effects reported by Egly et al. is that attention automatically 'spreads' outward from the cued location and ends abruptly at the contours of the cued object (Abrams and Law 2000; Egly et al. 1994). However, Shomstein and Yantis (2002, 2004a) have argued that sensory enhancement does not necessarily spread to object boundaries. Based on their interpretation of the Egly et al. findings, the uncued end of the attended rectangle receives higher priority than the uncued end of the unattended rectangle, and therefore is searched first on invalid trials (resulting in faster reaction times). However, if a location within a cued object is reliably irrelevant, it will not be afforded attentional priority. Consistent with this claim, Shomstein and Yantis (2002) found that distracting flankers had equally deleterious effects on subjects' ability to report the identity of a target letter, regardless of whether or not the flankers appeared on the same object as the target (but see Kramer and Jacobson 1991). In a related study, Shomstein and Yantis (2004a) presented subjects with displays similar to those used by Egly et al. while manipulating the amount of time separating the onset of the cue and target displays (referred to as the stimulus onset asynchrony or SOA). Same-object

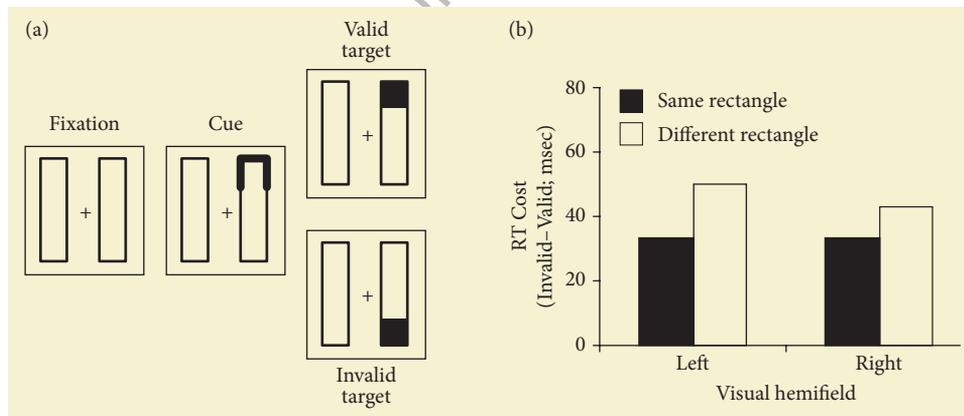


FIGURE 20.4 (a) Schematic representation of the task used in Egly et al. (1994). The thick black contours in the middle panel represent cues, while the black squares in the final panel represent targets. During invalidly cued trials, the target could appear on the opposite end of the cued rectangle ('same-object' trials) or on the same end of the uncued rectangle ('different-object' trials). (b) Depiction of the mean costs of invalid cueing (defined as invalid-valid cue reaction time, or RT) as a function of invalid cue type (same rectangle shown in black; different rectangle shown in white) and the visual hemifield that contained the target.

advantages similar to those reported by Egly et al. were observed when the cue-to-target SOA was low (200 or 400 ms), but not when it was high (600 ms). This result suggests that attention may initially prioritize whole objects before contracting to encompass only specific cued locations.

Additional evidence for object-based selection has been reported in the multiple-object tracking (MOT) literature. In a typical MOT task, subjects are cued to track a number of independent targets as they move across the display; moving non-targets are also presented, thereby ensuring that subjects cannot select the entire display via a single spatial ‘spotlight’ (Pylyshyn and Storm 1988). Typically, this task becomes much easier when targets move in a co-linear or otherwise predictable manner, thereby allowing observers to group different targets into a single object (e.g. a single moving square or other polygon; Yantis 1992). It is worth noting that these findings may reflect operations of OBA and/or SBA, as multiple studies have demonstrated that spatial attention may be directed to discrete regions of space without spreading to intervening locations (Awh and Pashler 2000; McMains and Somers 2004). In a related study, Blaser, Pylyshyn, and Holcombe (2000) created a task where subjects tracked stationary objects as they moved through *feature* space in order to remove any SBA contributions. Subjects were shown two spatially superimposed Gabor patches that moved along different trajectories in orientation, colour, and spatial frequency space while remaining fixed in the centre of the screen. To discourage a feature-based tracking strategy, the trajectories of both Gabors were random and independent such that the stimuli frequently ‘crossed paths’ in feature space. Despite this, subjects were able to track the target Gabor with very high accuracy. In a second experiment using similar displays, subjects detected small discontinuities in one or two stimulus attributes (e.g. a sudden displacement in colour or orientation) on the same or different objects that occurred at unpredictable intervals during the tracking period. The results of this study were nearly identical to those reported by Duncan (1984): specifically, subjects were equally good at detecting either one or two feature displacements within a single object, but were relatively poor at detecting feature displacements on different objects.

Neural evidence for and models of object-based attention

The available evidence suggests that—like FBA—OBA modulates stimulus representations across early stages of the visual processing hierarchy. For example, Wannig, Rodriguez, and Freiwald (2007) recorded from neurons in cortical area MT+ while monkeys performed a surface discrimination task. At the beginning of each trial, a colour cue indicated which one of two superimposed rotating (i.e. clockwise vs counter-clockwise) kinetograms to attend. Neurons in MT+ responded more strongly to their preferred direction of motion when it corresponded to the attended relative to the unattended surface. Similar changes in firing rates have also been documented in visual areas V1–V3a and V4 (Ciaramitaro, Mitchell, Stoner, Reynolds, and Boynton 2011; Fallah, Stoner, and Reynolds 2007). Because both surfaces occupied the same spatial location,

these findings cannot be explained by a selection mechanism that enhances the cortical representation of all stimuli within a given aperture.

At the cortical level, Duncan (1998) has proposed that OBA results from an integration of competitive interactions across multiple feature-selective modules. According to this integrative competition model, when an observer directs attention to one feature of an object (e.g., colour), mechanisms of selective attention bias ongoing competitive interactions in cortical modules that process this feature as well as the remaining features (e.g. orientation, motion, spatial frequency) of the same object. As a result, the neural representations of all the object's features are enhanced. This perspective is supported by multiple electrophysiological and neuroimaging studies in humans. In one such study, O'Craven, Downing, and Kanwisher (1999) presented subjects with arrays containing superimposed images of faces and houses. On each trial, either the face or house image moved along one of four axes. In separate blocks, subjects were instructed to attend the identity of the face image, the identity of the house image, or the direction of the moving image with the goal of detecting trial-by-trial repetitions of the relevant attribute. The authors examined changes in the amplitude of the BOLD response observed in cortical regions selective for faces (the fusiform face area or FFA), houses (the parahippocampal place area or PPA), and motion (hMT/MST) as a function of what attribute subjects were instructed to attend. The results revealed that attending to one attribute of an object was not only associated with a greater BOLD response in the cortical area selective for this attribute, but also in the cortical area selective for the other, irrelevant attribute of the same stimulus. For example, while subjects detected repetitions in the moving faces array and ignored superimposed houses, both FFA and hMT/MST were activated, while PPA was not. Similarly, Schoenfeld et al. (2003) found evidence for preferential processing of an attended object's behaviourally irrelevant features using EEG and fMRI. Here, subjects were instructed to attend to one of two superimposed white dot kinetograms that were distinguishable by their direction of motion (leftward or rightward) and detect brief changes in speed. On a subset of trials, the dots within the attended or unattended kinetogram changed colour from white to an isoluminant red. Spatiotemporal analyses of event-related potentials and the BOLD signal revealed a rapid increase in neural activity within colour-selective regions of fusiform gyrus when the attended kinetogram changed colour (~50 ms following the initial registration of colour information in the same cortical area) that was not observed for similar colour changes in the unattended kinetogram. These findings suggest that OBA enhances neural responses to both relevant and irrelevant object features in a rapid manner, consistent with the integrated competition model of OBA proposed by Duncan (1998).

The integrated competition model also predicts that the cortical representation of unattended objects should be suppressed (relative to the representation of the attended object), and there is some evidence to support this (Khoe, Mitchell, Reynolds, and Hillyard 2005; Pinilla, Cobo, Torres, and Valdes-Sosa 2001; Valdes-Sosa, Bobes, Rodriguez, and Pinilla 1998). Valdes-Sosa et al. (1998) recorded EEG while human subjects attended to one moving kinetogram (defined by colour) to detect brief perturbations in its rotational direction, while ignoring task-irrelevant perturbations in a

superimposed, unattended kinetogram (defined by a different colour). In one condition, the two fields were made to rotate in opposite directions, resulting in a percept of two transparent surfaces sliding across one another ('two-surface' condition). In a second condition, both kinetograms rotated in the same direction, yielding a percept of a single multicoloured object ('one-surface' condition). Attention effects were quantified by comparing the amplitudes of early, visually evoked potentials (the P₁/N₁ complex) observed approximately 100 ms following a perturbation of the attended or unattended fields. In the two-surface condition, P₁/N₁ amplitudes were substantially smaller following a perturbation of the unattended relative to the attended field. Critically, this effect was eliminated in the one-surface condition: P₁/N₁ amplitudes were statistically equivalent for either field, each reaching the same level of attended fields in the two-surface condition. Together, these results suggest that processing of superimposed, irrelevant sensory information can be suppressed in favour of relevant information when each can be perceived as belonging to distinct objects.

Control of object-based attention

In the previous section, we surveyed many studies suggesting that OBA (like FBA) modulates sensory representations across early stages of the visual processing hierarchy. Available evidence suggests that these modulations reflect top-down attentional control signals that originate in frontoparietal cortical areas (Friedman-Hill, Robertson, Desimone, and Ungerleider 2003; Olson 2003; Robertson and Treisman 2006; Serences et al. 2004; Shomstein and Behrmann 2006; Wojciulik and Kanwisher 1999). In one study, Serences et al. (2004) showed human subjects displays containing spatially superimposed face and house images (similar to the displays used by O'Craven et al. 1999, discussed in the last paragraph) that smoothly morphed every one second. Subjects were instructed to attend to the face or house images in order to detect occasional pre-specified target images. Two types of targets were presented: 'hold' targets instructed the subject to maintain attention on the current image category (e.g. faces), while 'switch' targets indicated the subject to switch attention to the other image category (e.g. from faces to houses). Event-related fMRI revealed transient increases in activation within several frontoparietal regions (including IPS, SPL, and superior frontal sulcus or SFS) immediately following the presentation of 'switch' relative to 'hold' targets, suggesting that these regions play an important role in mediating object-based shifts of attention. Interestingly, many of the same regions also showed transient increases in activation following shifts of SBA (e.g. Corbetta and Shulman 2002; Serences and Yantis 2006; Yantis et al. 2002), suggesting that a common attentional control network might mediate shifts of both spatial- and object-based attention. In a related study, Shomstein and Behrmann (2006) presented subjects with arrays similar to those used by Egly et al. (1994; see Fig. 20.4a) and examined transient changes in the BOLD response following instructions to shift attention to a different location of the same object, or an equidistant location on a different object. As in earlier work (e.g. Serences et al. 2004), activation within

regions of SPL increased transiently immediately following an instruction to shift attention. Moreover, activation in left SPL was substantially larger following within-object relative to between-object shifts, suggesting that this region is particularly important for object-based attentional selection. Similar to attentional control of feature selection, however, object-based attentional control is currently underexplored. Given the modest evidence that suggests some gross anatomical overlap across SBA, OBA, and FBA, future studies would benefit from utilizing MVPA methods to determine how sub-populations within the frontoparietal network may differentially control these selection mechanisms.

Limitations of existing object-based attention demonstrations

Although the findings reviewed in the preceding section are consistent with an object-based selection mechanism, many of these effects are also consistent with modified feature-based accounts, so caution is warranted before positing two entirely separate mechanisms of selection. For example, consider the findings reported by O'Craven et al. (1999), where directing attention to one attribute of a stimulus (e.g. the identity of a moving face image) enhanced the cortical response to other attributes of the same object (e.g. the motion of the image). Taken at face value, these results suggest that directing attention to one attribute of an object *automatically* leads to enhanced processing of all attributes of the object. However, these results can also be explained via the operation of a feature-based attentional mechanism. For example, in order to track the motion of the face image, subjects may have chosen to attend the eyes, mouth, or the face as a whole. Presumably, this strategy would result in an increased response in both face- and motion-selective cortical regions. On this point, it is worth noting that O'Craven et al. (1999) observed that neural responses to the task-relevant attribute were always stronger than those observed to the task-irrelevant attribute of the same object, consistent with the operation of feature selection. Moreover, the high accuracy with which subjects completed the task suggests it was not particularly attention-demanding; therefore, a second, parsimonious account is that attention was not fully engaged by the face, and that subjects voluntarily attended to the motion vector as well, which would certainly be within attentional capacity limits (see discussion of the Xu 2010 study in 'Interactions Between FBA and OBA' below). Likewise, recall that Wannig et al. (2007) demonstrated that neurons in MT+ responded more strongly to their preferred direction of motion when it was carried by an attended versus an unattended colour-defined surface. Although these findings are nominally consistent with the operation of a surface or object-based attentional mechanism, they can also be explained by putative interactions between spatial- and feature-based attentional mechanisms (see Treue and Katzner 2007). For example, rotating surfaces like those used in the study contain a large number of locally varying direction signals (e.g. for a counterclockwise-rotating surface, dots on the right will appear to move upward while those on the left will appear to move downward). When attention is directed to such a surface, neurons with receptive fields (RFs)

that cover only local patches of the surface will be modulated according to the match between the local direction inside the neuron's RF and the neuron's preferred direction of motion (e.g. Martinez-Trujillo and Treue 2004). Across multiple neurons, this will result in a position-dependent pattern of modulation that will selectively enhance processing of the currently attended direction of rotation.

In many studies purporting to document object-based selection, subjects were not explicitly discouraged from attending task-irrelevant features and therefore the extent to which OBA may be automatically deployed cannot be determined. Some studies have reported evidence for OBA even when such selection would offer no benefit to the observer, but neither was this selection necessarily detrimental (e.g. see discussion of O'Craven et al. 1999 above). A small number of studies, however, have shown evidence of OBA even when such selection was disruptive to the observer's goals. Both Kramer and Jacobson (1991) and Scholl, Pylyshyn, and Feldman (2001) found that subjects were less able to ignore distracting features when they belonged to the same object as the target. For example, Kramer and Jacobson (1991) found greater flanking effects when distracting flankers were connected with a central target, while Scholl et al. (2001) found in an MOT task that subjects were more likely to erroneously track a distractor when it belonged to the same object as a target. These data suggest that under some circumstances, OBA may be obligatory. Of note, however, Kramer and Jacobson (1991) found the largest effects when flanking distractors were near the central target (these effects were reduced as distance between stimuli increased); Scholl et al. (2001) found the largest effects when targets and distractors were difficult to differentiate into component parts. Thus, OBA may be automatically deployed when reducing an object into individual features is difficult or effortful.

INTERACTIONS BETWEEN FBA AND OBA

The evidence presented above on object-based selection runs counter to several studies discussed earlier that favour discrete feature selection (see 'Behavioural evidence for feature-based attention'): while OBA studies tend to show preferential selection for both relevant and irrelevant features of an attended object, FBA studies tend to show that only the neuronal representations of relevant features are enhanced (or at least are afforded a greater enhancement). Xu (2010) argues that these disparate results can be accounted for if one considers the capacity limitations of the attentional system. Various studies have converged on a capacity limit of approximately four items (Fisher 1984; Pylyshyn and Storm 1988; Scholl 2001), and there may be some cost associated with encoding multiple features of a given object (Woodman and Vogel 2008). In line with these previous findings, Xu (2010) found that neural responses to an irrelevant feature dimension were modulated only when the number of unique instances along an attended feature dimension did not exceed subjects' capacity. Here, subjects completed a colour visual short-term memory task in which they reported whether a test

colour was present or absent in a previously viewed array of six objects. The sample array of to-be-remembered information varied in the number of unique features present, including: one shape rendered in one colour, one shape rendered in six different colours, six shapes rendered in one colour, or six shapes rendered in six different colours (see Fig. 20.5a). As shown in Fig. 20.5b, fMRI responses in the lateral occipital complex (LOC) and the superior IPS were modulated by the number of unique colours present in the sample array. However, responses observed in LOC—a region from which responses have been linked to the relative complexity or ‘information load’ imposed by an array of to-be-remembered materials (e.g. Xu and Chun 2006)—were also modulated by the number of unique shapes present in the sample array. For example, responses observed when the sample array contained one colour and one shape were substantially lower than those observed when it contained one colour and six unique shapes. This difference was abolished, however, when the sample array contained six unique colours. Assuming that items containing six unique colours or shapes were enough to exhaust mnemonic resources, these data suggest that OBA is not always automatically deployed. Instead, the selection of task-irrelevant information may depend on task demands.

CONCLUSIONS

Throughout this chapter, we have generally followed the course of the existing literature by treating FBA and OBA as two distinct selection mechanisms. This separation makes intuitive sense: FBA operates entirely on elementary properties coded by the early visual system, such as colour, shape, orientation, and motion, while OBA can operate on more complex representations such as faces and houses. A second obvious and potentially critical difference between studies of FBA and pure OBA is the spatial extent of modulation. Both psychophysical and neuroimaging studies have reliably established that feature selection globally recruits relevant sensory populations, even those outside the locus of spatial attention (Andersen et al. 2009; Rossi and Paradiso 1995; Serences and Boynton 2007; White and Carrasco 2011), whereas OBA demonstrations are typically restricted to the attended object. However, recent research suggests that at least under some circumstances, OBA may spread to cortical regions with strong foveal biases (e.g. Williams et al. 2008; Williams, Dang, and Kanwisher 2007), although not across the entire field. Thus, even if there is some spatial spread of OBA, it appears to be distinct from the more global spread of FBA, suggesting a mechanistic distinction between these two forms of selection.

Nonetheless, the distinction between FBA and OBA is not entirely clear-cut, and it is not always trivial to classify a single study as evidence in support of one form of selection over another. The main theoretical distinction between feature-based and object-based selection is whether relevant and irrelevant features are afforded a similar attentional benefit when they belong to the same object. However, even this simple distinction breaks down in studies of global feature-based attentional spread, as FBA may sometimes spread from a relevant feature to a paired irrelevant feature, even if they occur

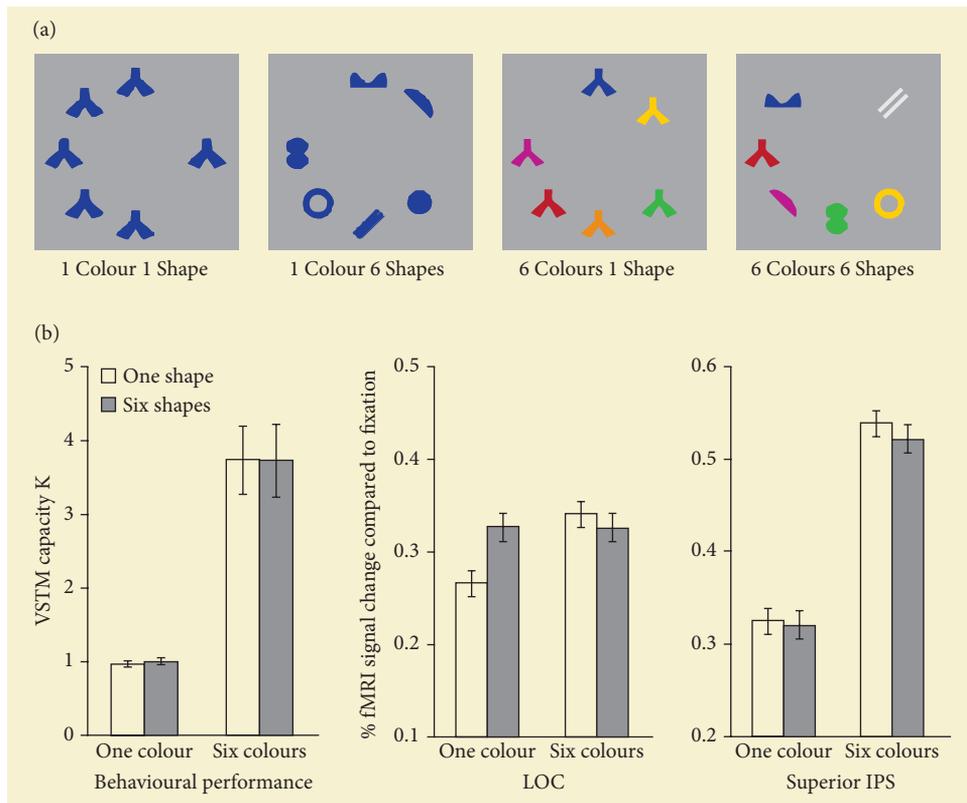


FIGURE 20.5 (a) Schematic of the stimulus arrays used in Xu (2010). Display complexity was manipulated by varying the number of unique colours within the sample array (one or six, respectively). (b) Left panel: Visual short-term memory capacity was modulated by the number of unique colours in the display, but was unaffected by the number of unique shapes. Middle and right panels: fMRI responses in lateral occipital complex (LOC) and superior intraparietal sulcus (IPS) were modulated by the number of unique colours present in the sample array. However, in LOC—where the magnitude of neural responses has been linked to the relative complexity or information load imposed by an array of to-be-remembered information—responses were also modulated by the number of unique shapes in the sample array when only one colour was present. Xu interpreted these findings as evidence for a flexible object-selective encoding mechanism. When processing resources have been exhausted (e.g. when subjects were asked to remember six unique colours) then neural responses to behaviourally irrelevant features (e.g. shape) are attenuated.

together outside the spatial focus of attention (Arman et al. 2006; Melcher et al. 2005; Sohn et al. 2005). In fact, here we have reviewed a myriad of studies that have shown single feature selection (1) entirely at the expense of paired irrelevant features; (2) in conjunction with modest (albeit comparatively reduced) representation of paired irrelevant features; and holistic object selection, in which all features are afforded similar levels of cortical representation.

Given this apparent gradient from single feature to full object selection, we argue against two completely independent attention mechanisms and particularly against

the automatic nature of object-based selection. Instead, we propose that relevant information is flexibly selected according to task demands, and that the interplay between observer goals and the nature of the physical display will dictate the nature of selection across the set of features that combine to make an object (see Kravitz and Behrmann 2011). For example, FBA can violate the tenets of OBA when extreme emphasis is placed on accurately characterizing a single feature of a multi-part object. In these cases OBA may *not* be automatic or obligatory, but rather *can* occur when selection demands are not high and no cost is incurred for selecting all the features on an object. Finally, although object-based attention does not appear to be automatic, it may be the rule rather than the exception in many cases where holistic processing is critical for identifying relevant information, such as when searching for a face in a crowd (Richler, Tanaka, Brown, and Gauthier 2008; Tanaka and Farah 1993). In this situation, FBA might still be possible, but relatively useless given processing demands. While each of these questions merits further investigation, the emerging consensus is that feature-based and object-based attentional mechanisms are not distinct systems in any absolute sense. Instead, they operate along a continuum and the extent to which selection is based on a specific feature or an object depends on both the complexity of the stimulus array and on the specific behavioural goals of the observer.

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