Does fMRI Contribute to Vision Science?

Task-Dependent Activation Within Visual Areas

Matthew L. Nielsen

Brain Function Research Group, Kansai Advanced Research Center,
Communications Research Laboratory, Ministry of Telecommunication and Posts
588-2 Iwaoka, Iwaoka-cho, Nishi-ku, Kobe 651-2401, Japan

1. Introduction

In the early years of functional magnetic resonance imaging (fMRI), vision researchers were delighted to show a reproducible stimulus-activation relationship within a given visual area or areas. Common examples include retinotopic activation of lower visual areas by flashing checkerboard patterns, and activation of the MT/V5 complex by motion stimuli. However, recent research has revealed that such activation is not the result of a simple stimulus-activation relationship. Rather, the magnitude of the activation changes depending on the task performed while viewing the stimulus, even when the stimulus itself does not change. Such activation is termed "task-dependent." Thus, the relationship which must be characterized for a given visual area is really a task-stimulus-activation relationship. The primary purpose of this paper is to review recent attempts to characterize such relationships using fMRI. Integral to such characterizations is a consistent and adequate method of localizing visual areas, so a section of this introduction will be devoted to that topic.

1.1 Functional MRI and data analysis

The technical foundations of fMRI and the analysis methods for resulting data are described in other articles of this volume, so they will not be covered in detail here. Suffice it to say that many analyses are possible, and every study reviewed here represents a different method. To provide an overview of this breadth, the general analysis method for each study will be mentioned briefly (cross correlation, t test, Kolmogorov-Smirnov (KS) statistic, etc.). Except where noted, all reported activation is significant to at least $p<0.05$, corrected for multiple comparisons by the Bonferroni method.

Except for a couple of cases, all of the reviewed studies were conducted with 1.5 Tesla MRI systems. Studies conducted with higher-field machines will be noted since they may provide higher significance levels or additional activation sites when compared with 1.5 Tesla studies.

1.2 Task-dependent activation

Why is task-dependent activation interesting? Because it shows that visual cortex is not simply a collection of processing modules, each extracting information and passing it on to higher-level modules or higher brain areas ("bottom-up" only). Rather, those higher brain areas seem to be controlling individual visual areas, instructing them as to which features to extract and where to extract them from ("top-down"). Such control is presumably mediated through a multitude of top-down connections which have been found throughout visual cortex, projecting from cognitive areas to higher visual areas, and from higher visual areas to lower visual areas[1,2]. Within each visual area, the cognition (task)-driven and stimulus-

driven signals meet and interact, producing activation which depends on both[3-5]. In the following review, there are many examples of such activation in extrastriate and even striate visual cortex, compatible with "early selection" theories of visual attention such as that of Treisman and Gelade[6].

Most work in this area involves tasks which manipulate attention, that is, two tasks are designed so that the major difference between them is a different state of visual attention. Usually, the stimuli are identical between the two tasks. Thus, the conclusion can be drawn that any change in neural activity within visual areas must be due only to the change in task, or if properly designed, the change in attentional state. Task-dependent activation has also been found using tasks which do not manipulate attention. To the author's knowledge, the only examples are in the field of mental imagery. In these studies, the experimental task requires some kind of mental visualization, while the control task does not. Before beginning the review, one important topic must be discussed, that of identifying activated areas in a consistent and adequate manner.

1.3 Functional localization of visual areas

Typically in functional neuroimaging, activated areas are identified and compared across studies by transforming data into the coordinate system of Talairach and Tournoux[7]. Then researchers can discuss activated sites in terms of Talairach coordinates, or in terms of Brodmann's areas (BA) defined in Talairach coordinates. Within visual cortex, however, this is usually inadequate due to variation in anatomical location of visual areas across individual subjects. This anatomical variation has been quantified in a PET study which located the borders of occipital visual areas[8]. Therefore, vision researchers find it necessary to localize visual areas based on their function. "Localization" in this context must include some notion of extent, that is, defining the borders of a functional area.

1.3.1 Example: the motion-processing area hMT/V5

A straightforward and common example is the localization of the motion-sensitive MT/V5 complex by presenting a moving random-dot stimulus. Comparison of fMRI signals resulting from this and a stationary dot pattern provides strong differential activation near the occipitotemporal junction in humans[9,10]. This is defined to be MT/V5, corresponding to the medial temporal area in the monkey. Although "MT" is a term based on monkey neuroanatomy, it seems to be more widely used in the literature than "V5." Some authors have used the term "hMT" to avoid ambiguity (e.g., Beauchamp et al.[11] and Cornette et al.[12]), and that term will be used hereafter in this paper. Depending on the exact paradigm, other motion-processing regions may also be activated, including V3A, the lingual gyrus, and the human homologue of MST (hMST)[5,12]. Often, hMST cannot be distinguished from hMT due to its small size and the effective spatial resolution of fMRI. In such cases, the combined area will be referred to as the hMT complex, or simply "hMT+."

1.3.2 Border Mapping

An alternative to defining areas based on responsiveness to a particular stimulus (such as random-dot motion for the hMT complex) is the border-mapping method first applied by Sereno et al.[13] This method is based on the fact that lower visual areas are organized retinotopically, and that adjacent areas are mirror images of one another. This produces a spatial and processing hierarchy, with each consecutive area being a mirror image of its predecessor (Fig. 1). This convenient organization was combined with a stimulus that maps the two dimensions of the cortical retinotopy (eccentricity and polar angle) and computational techniques which warp and flatten the cortical

sheet. After converting the data to a two-dimensional sheet, the borders between neighboring visual areas can be located by an algorithm which traces the mirror-reversals in retinotopic organization. The result is a powerful tool for mapping the visual areas of occipital cortex.

2. Attention-induced task-dependent activation

As noted in the introduction, many studies which obtain task-dependent activation depend on a change in attentional state between two tasks. This section will include sub-sections devoted to different types of attention. The first type is general visual attention contrasted with attention to other modalities. Following that, visual attention will be subdivided into featural attention (motion and non-motion features), spatial attention, combined featural and spatial attention, and "high level" attention to a complex object. Each study contains two or more different tasks (conditions). To help

avoid confusion, all task names are printed in italics.

2.1 Modality attention

Perhaps the simplest manipulation of visual attention is the shifting of attention between vision and another modality. Such modality attention shifts have been investigated with fMRI in visual-auditory and visual-somatosensory paradigms.

In a study by Woodruff et al.[14], subjects were presented with simultaneous, visual-auditory stimulus pairs. Specifically, the stimuli were pseudo-random numbers, presented every 1.7 s such that the visible and audible numbers in each pair were always different. The six-minute experiments were divided among three conditions: (1) *"attend visual numbers,"* (2) *"attend auditory numbers,"* and (3) *"fixate on the fixation point."* To verify that the task was performed correctly, subjects were instructed to press a button every time they detected the number 8 (a visible 8 in
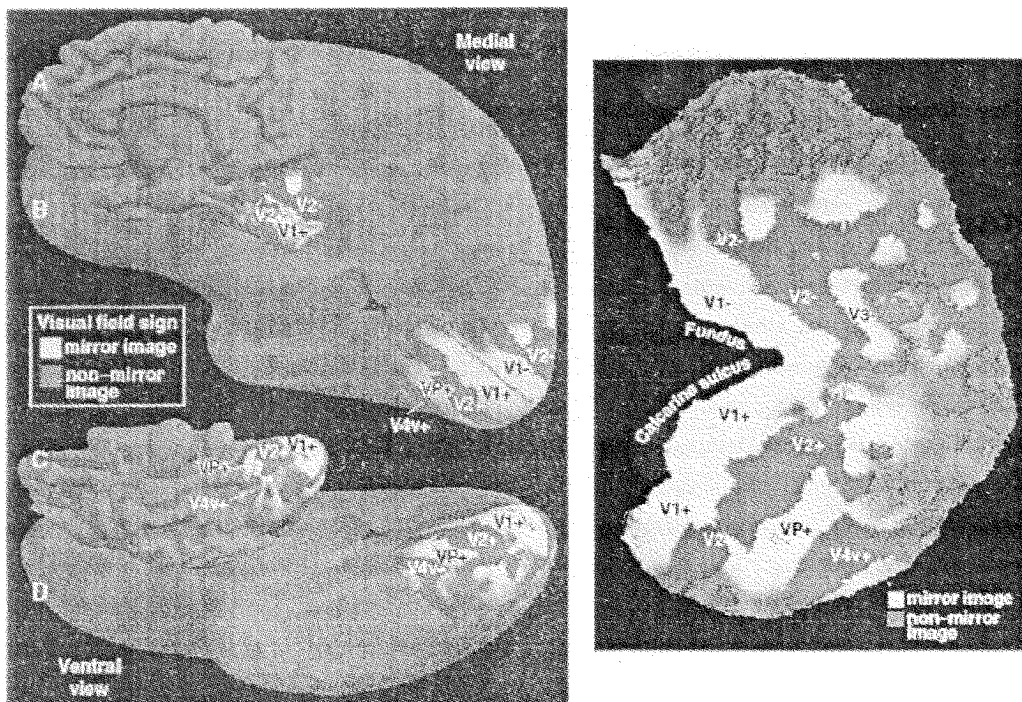

Fig. 1   Border mapping (reproduced from Sereno et al.[13]). *Left.* A and C show the cortex in its natural form. B and D show an inflated display format. *Right.* Occipital cortex in a flattened format showing borders between lower visual areas.

"attend visual" conditions and an audible 8 in *"attend auditory"*). The KS statistic[15] was used to determine significant differences in MR signal between the two "attend" conditions within individual pixels (p<0.001, uncorrected for multiple comparisons). Average signal differences (for four subjects) in extrastriate visual cortex (BA 18, 19, 37 & 39) just failed to reach significance, with p<0.15. No difference was apparent in primary visual cortex (BA 17). Auditory attention, however, enhanced the signal in auditory association areas (BAs 21 and 22; p<0.058 and p<0.045, respectively). Higher significance levels were obtained in auditory cortex (including primary auditory cortex) with a surface coil placed over the left temporal region. The authors suggest that the observed modulation may be due to enhanced neural activity in sensory cortex during corresponding attention conditions, or to decreased activity in regions subserving the other modality.

Haug et al.[16] sought to estimate the extent of hMST (which they call V5A), and as a secondary objective, to gauge the effect of modality attention on its activity. They employed a novel stimulus, a rotating, sine-modulated windmill, thereby eliminating some non-motion stimulation found in previous authors' paradigms. The windmill started and stopped alternately in a motion condition and remained stationary in a rest condition. In one paradigm called *"focused attention,"* only visual stimulation was applied, and subjects were instructed to mentally count starts and stops of the rotating windmill during the motion condition, while fixating on the center. In another paradigm called *"distracted attention,"* visual and electrical stimulation were combined. Electrical stimulation was applied to the right wrist at two current levels, occurring randomly, and subjects were instructed to mentally count the number of high-current stimuli. Data were analyzed by cross correlation (CC) with an ideal square-wave response function

defined for the motion and rest conditions. As intended, the novel stimulus did not activate lower visual areas, leaving a single activated area at the occipital-temporal-parietal junction corresponding to hMST. In ten out of ten subjects, the *focused attention* paradigm produced hMST activation above a CC threshold of 0.4-0.5 with an average volume of 76 cubic mm (4 bilateral, 3 left only, 3 right only). This area was taken as the functional definition of hMST in each subject. In the *distracted attention* paradigm, fewer hMST pixels were activated at the same threshold in all subjects, completely disappearing in two. This decrease was significant to p<0.01 using the signed rank statistic.

A common result is apparent in these two studies of modality attention: during attention to the visual modality, visual cortex activity is higher than during attention to another modality. This may be due to either enhancement or suppression of neural activity by attention, as noted by Woodruff et al.[14] In Haug et al.'s study[15], however, we cannot conclude conclusively that the reduced activation during *distracted attention* was due to an attention difference since electrical stimulation was not applied during the *focused-attention* condition.

2.2 Featural attention

A more sophisticated aspect of visual attention is attention to a specific feature such as color, orientation, motion direction, or motion speed. A foundational study in this area was a PET study by Corbetta et al.[16] They investigated two attentional strategies: (1) *selective attention* to one of three visual features (speed, color or shape), and (2) *divided attention* distributed among the three features. Their stimuli consisted of 30 translating, colored rectangles, and the task was a same-different discrimination in which any of the features could change on a given trial. Button presses were used to verify that the correct attentional strategy was actually performed. Passive blocks, with stimuli identical to the attention blocks, were also

included in which subjects were to only fixate and not attend or respond. For each of the two attentional strategies, distinct, non-overlapping patterns of activation were observed in extravisual brain areas when compared to passive blocks. *Divided attention* activated the anterior cingulate and dorsolateral prefrontal cortex. *Selective attention,* on the other hand, activated the globus pallidus, caudate nucleus, lateral orbitofrontal cortex, posterior thalamus/ colliculus, and insular/ premotor cortex. In addition, during *selective attention*, specific areas of extrastriate cortex were activated, depending on the specific feature being attended. These results suggest that distinct neural sub-systems within non-visual brain regions mediate different attentional strategies, and that these sub-systems "tune" specific, extrastriate visual areas when a specific feature is required in a task.

Many recent fMRI studies of featural attention involve features of motion such as speed and direction. Therefore, the following review of featural attention results will be divided into two parts, the first covering non-motion types of features and the second covering motion features.

2.2.1 Featural attention: non-motion

Le, Pardo and Hu[18] recently employed a paradigm similar to that of Corbetta et al.[17] using the 4-Tesla fMRI machine at the University of Minnesota. Rather than selective versus divided attention, they were interested in *sustained* versus *shifting* attention (all selective). Each stimulus was either a circle or square, displayed in red or green at the fixation point. The *sustained-attention* task required subjects to attend to only color, or only shape, for 70 s. The *shifting-attention* task required subjects to shift attention between color and shape every 3 s, on average. Subjects were to press a button every time they detected a target (always red for color attention, a circle for shape attention, and alternating after every detection for *shifting*

attention). Again, the stimuli were statistically identical across blocks, including a *fixation only* condition. In voxel-wise *t* tests of *shifting* versus *sustained* attention, significant differences in MR signal were found in the posterior superior parietal lobule, the cuneus and precuneus, and the folium and ansiform lobule of the cerebellum (*shifting* > *sustained*). In comparisons of *sustained attention* to *fixation*, as in the similar selective-attention conditions of Corbetta et al.[17], differing patterns of activation were observed in extrastriate cortex depending on whether attention was to color or shape. One might also expect some similarities between the *shifting-attention* activation here and the divided-attention activation of Corbetta et al. (anterior cingulate and dorsolateral prefrontal cortex). However, Le et al.'s slices did not include the frontal lobe, and Corbetta et al. likely did not analyze the cerebellum. Thus, the only certain differences are in the posterior superior parietal lobule, the cuneus, and the precuneus, all activated by Le et al.'s *shifting attention* task. Therefore, one interpretation is that these areas are important to rapidly shifting among feature-selective attention states, but not important to a divided attention state.

In a study focusing on only one visual feature, orientation, Orban et al.[19] employed foveal grating stimuli. This was a PET study which was later extended to include fMRI in a similar paradigm with a motion attribute, so it will be briefly reviewed here. The tasks were (1) *passive viewing,* (2) *grating detection,* (3) *orientation identification,* and (4) same-different *discrimination of successive gratings.* There was little difference among the first three conditions, which activated striate and near extrastriate cortex, extending into the middle fusiform gyrus. The *successive discrimination* task, however, evoked significantly more activation in the middle fusiform gyrus than did the *identification* task.

2.2.2 Featural attention: motion

The last non-motion study was extended by the same group to the feature of motion direction using a translating random dot display, and both PET and fMRI[12]. The purpose was to gain further evidence for task-dependent activity and functional specialization within visual cortex. They used essentially the same four tasks as in the grating study, i.e., (1) *passive viewing*, (2) *motion detection*, (3) motion *direction identification,* and (4) same-different *discrimination of successive motion directions.* In addition, they added two non-motion detection tasks: fixation point *dimming detection* and *tone detection.* The stimulus configuration, including the random dots, fixation point dimming, and tone burst, was identical in all tasks. The PET results of *successive discrimination* minus *motion detection* yielded significant activation in the right fusiform gyrus, right lingual gyrus, right frontal operculum, left inferior frontal gyrus, and right thalamus. The tighter comparison of *successive discrimination* versus *direction identification* showed activation only in the fusiform and opercular sites, indicating their involvement in temporal comparisons. For ethical reasons, the number of PET conditions was limited to six, thus making it impossible to functionally localize motion processing areas in the same subjects. This is classically done by contrasting the activity produced by passive viewing of moving random dots versus stationary random dots[9,10]. Consequently, fMRI was used to functionally localize motion areas as well as collect additional data for some of the PET conditions (but only *successive discrimination* and *dimming detection* were used due to poor subject performance in the other conditions). The moving-versus-stationary comparison provided a functional definition of hMT, as well as bilateral activity in V3A, the lingual gyrus, and a posterior satellite region of hMT. In the *successive-discrimination*-versus-

dimming-detection comparison, there was no modulation in hMT. This comparison did, however, yield activation in the lingual gyri, the right fusiform gyrus, the right occipital gyrus (probably V3A), and the superior parietal lobe, in both the PET and fMRI data. The right fusiform activation is consistent across all comparisons of *successive discrimination* with other tasks, as well as with the successive discrimination of oriented gratings used by Orban et al.[19]

Buchel et al.[5] studied attention to motion speed instead of motion direction in a radial-motion random dot display. Their conditions were (1) *fixation point only,* (2) *stationary dots,* (3) *passive viewing of moving dots,* and (4) *attention to the speed of moving dots.* The stimulus was identical in the latter two conditions, allowing conclusions to be made about attention-dependent effects. In the *attention* condition, subjects were asked to "detect speed changes" without responding or counting, and in the *passive* condition they were asked to "just look." Following the experiment, subjects were asked to make a *post hoc* estimate of the number of speed changes. Functional images were acquired with a 2 Tesla MRI system and analyzed with SPM96[20] to provide a *t*-statistic for every voxel. Area hMT was functionally localized within the occipitotemporal junction using the *moving*-versus-*stationary* comparison. In addition, activation was found in the middle occipital gyrus in an area believed to be V3A (by comparison with DeYoe et al.[21] and Tootel et al.[22]). In the task-varying comparison, *attention* versus *passive viewing,* activity appeared in several areas spanning occipital, parietal, and frontal cortex, and borderline significant activity was found in the thalamus. Occipital activation was found in the lingual gyrus (anatomically, the area of the V1/V2 border), in the middle occipital gyrus (same as the functional localization, probably V3A), and just inferior to hMT (about 10 mm below the peak of

the functional localization).

O'Craven et al.[23] used a display containing superimposed stationary and radially moving random dots. The conditions were *"attend to the moving dots"* and *"attend to the stationary dots,"* but the stimulus was identical in both. Data were analyzed by applying the KS statistic to each voxel. All regions of interest (V1, V2, and hMT+) were localized by comparing activity from passive viewing of moving versus stationary random dots. The peak of activation at the temporal-parietal-occipital junction was taken to be hMT+, while a second dorsomedial area of activation was assumed to be V1 and V2. Activation in the hMT complex was significantly higher during *attend moving* than during *attend stationary*. No change in activity associated with attention was observed in the combined V1-V2 area.

Watanabe et al.[24] used a similar stimulus with overlapping translating and radially moving random dots. The conditions were *"attend to translation"* and *"attend to radial motion,"* while again, the stimulus was identical in both. V1 was localized using a retinotopy mapping method[25] less complicated than that of Sereno et al.[13], while hMT+ was localized using the usual method of moving versus stationary random dots. Activation in hMT+ was significantly higher during *attend radial motion*. However, activation in V1 was significantly higher during *attend translation*.

While O'Craven et al.[23] showed motion-attention enhancement of hMT+ for radial motion, Watanabe et al.[24] demonstrated greater enhancement for attention to radial motion than for attention to translation motion. In addition, they provide evidence for motion-attention modulation in V1, which they claimed first in a separate article[26]. These studies are not contradictory since O'Craven et al. used only radial motion, and not translation.

2.3 Spatial attention

Without moving the head or eyes, it is still possible to direct attention to a specific area of the visual field, distinct from the point of gaze defined by eye position. This is the focus or "spot light" of spatial attention. Treue and Maunsell[27] found that spatial attention affects the motion responsiveness of MT cells in monkeys.

Gandhi et al.[28] sought to demonstrate the effect of spatial attention in human V1. Their stimulus was a pair of moving gratings restricted to two circular apertures, centered 7 deg to the left and right of a central fixation cross. During each trial, two grating speeds (one slightly faster than the other), were presented in each aperture for intervals of 750 ms each. Subjects attended to either the *left* or *right* aperture based on a small cue presented at the fixation point, switching sides every 18 s. The task was to report which interval contained the fastest motion, first or second. The order of speeds was independently randomized for each aperture, and the speed increment was individually chosen so that all subjects performed with an accuracy of approximately 78%. In addition, a reference experiment was conducted in which the above stimulus was alternated with a uniform field every 18 s. The task was central fixation. V1 was functionally localized using the method of Sereno et al.[13] During the attention and reference tasks, V1 response was quantified as the phase and amplitude of the sinusoid which best fit the average timecourse of V1 pixels. The amplitude in both hemispheres during the attention task was about 20% of the reference-task amplitude. The sinusoidal responses in left and right V1 were 180 deg out-of phase, with peaks time-locked to attention in the contralateral aperture. Since the attention-task stimulus was constant throughout the experiment (except for random speed changes), the only possible source of the sinusoidal modulation was the *left-right* alternation of spatial

attention.

2.4 Combined spatial and featural attention

Beauchamp, Cox and DeYoe[11] investigated the combined effects of spatial and featural attention in one study. They presented moving, colored random dots within an annulus centered on the fixation point. In test conditions, the annulus was defined by colored dots and coherent motion direction in a background of white, incoherently moving dots. The left and right semi-annuli contained dots with differing color and motion direction (Fig. 2). In control conditions, the entire display was filled with white, incoherently moving dots. In three separate test conditions, subjects were required to press a button reporting the following information, respectively: (1) which semi-annulus contained faster-moving dots, (2) which semi-annulus contained yellow dots, and (3) whether the fixation square increased or decreased in brightness. In (1), spatial and featural attention were directed to motion within the annulus ($S+F+$); in (2), spatial attention was still directed within the annulus, but featural attention was directed away from motion ($S+F-$); in (3), both spatial and featural attention were directed away from motion in the annulus ($S-F-$). During control conditions (white, incoherently moving dots), subjects responded randomly at the same rate as in the test conditions. The hMT complex was defined as the volume of peak differential amplitude in the $S+F+$ (versus control) activation map. Activation in other conditions was expressed relative to this, in terms of both amplitude and volume. In the $S+F-$ map, the amplitude and volume of hMT+ activation fell to 64% and 35% respectively. In the $S-F-$ map, these became 40% and 9%. These results
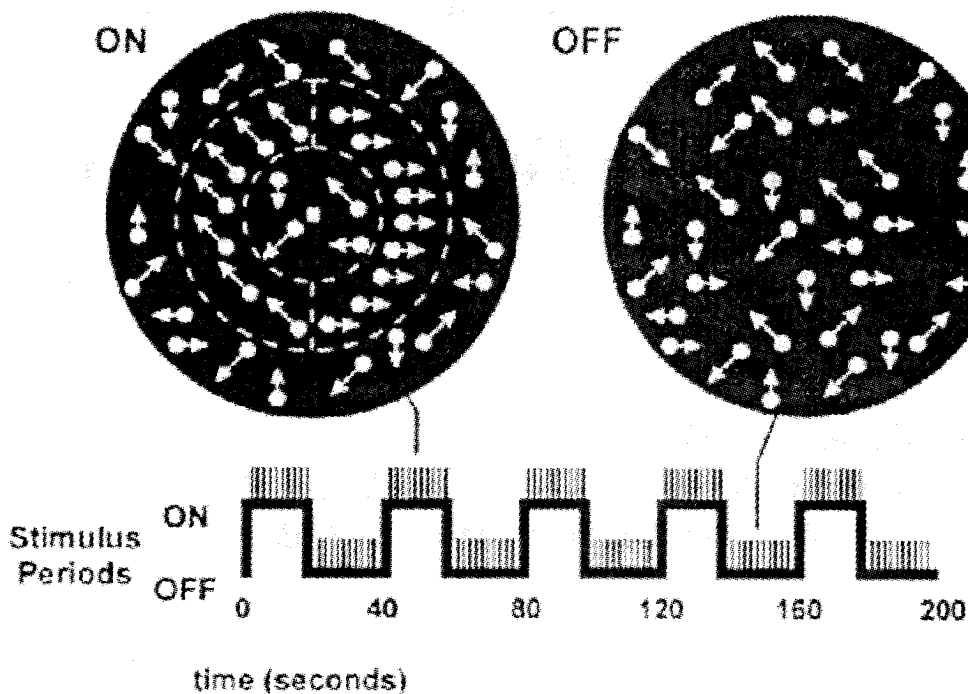

Fig. 2   The stimulus of Beauchamp et al. [11] for manipulating featural and spatial attention. The "ON" display is schematic for all attention conditions. The left and right sides of the annulus contained dots of different colors and with different motion directions. In separate conditions, attention was directed to motion direction ($S+F+$) or color ($S+F-$) within the annulus, or to the fixation square at the center ($S-F-$). The dotted lines did not appear in the actual stimulus.

demonstrate that both spatial and featural attention can modulate the motion responsiveness of hMT+, and that their effects can reinforce each other.

2.5 "High-level" attention: faces & places

The next study is given its own section because it does not address spatial attention or attention to low-level features such as those discussed previously. Rather, subjects performed a task in which they attended to either faces or houses, so one might consider the resulting attention to be a type of high-level attribute attention. The faces and houses were presented in different retinotopic locations within a given trial, but only for 200 ms, so saccades to the relevant locations were impossible. It is unclear to this author whether spatial attention could be oriented so quickly. Thus, in my opinion, the observed effect may be due in part to relocation of spatial attention to the relevant objects, or completely due to "high-level attribute attention." That said, Wojciulik, Kanwisher and Driver[29] sought to determine the task-dependence of activity in the fusiform face area (FFA), previously considered to be a task-independent processing module invoked whenever faces are presented to the visual system. Before the primary experiment, they functionally defined the FFA as the ventral occipitotemporal region that responded more strongly to faces than to other visual objects under passive central viewing. This area then served as the region of interest in the primary experiment. Each stimulus consisted four pictures, two faces and two houses, arranged symmetrically around the fixation point and presented simultaneously for 200 ms. In each trial, subjects performed a same-different discrimination task on either the faces or the houses while maintaining central fixation. Data were analyzed with the KS statistic[15]. Activity in the pre-defined FFA was significantly higher during the *face discrimination* trials than during the *house discrimination* trials. Wojciulik et al. make the point that despite the FFA's modular nature (functional specificity and anatomic localization), face processing within the module nevertheless depends on voluntary attention.

3. Imagery-induced task-dependent activation

The simplest type of mental imagery can be done anywhere by simply closing one's eyes and imagining some visual object or scene. A more complex type of mental imagery occurs when we look at a physical object and manipulate it mentally, e.g., mental rotation. Each of these has been studied using fMRI.

D'Esposito et al.[30] located areas activated by mental imagery of spoken words. Words were chosen from a dictionary and assigned to a *concrete* condition if they were easy to visualize ("apple," "house," etc.) and to an *abstract* condition if they were difficult to visualize ("treaty," "tenure," etc.). During *concrete* conditions, subjects were instructed to imagine the appearance of the named object (one per second), and during *abstract* conditions, they were instructed to passively listen to the words. An audible tone separated the conditions. Strictly speaking, we cannot say that resulting activation is task-dependent since the stimuli (words) were from different categories. However, they differed only at the semantic level in that the *concrete* words were easier to visualize. Physically, the chosen words were statistically identical between the trials. In that sense, the results are task-dependent. Data were analyzed by voxel-wise *t* tests, and Brodmann's areas were defined based on Talairach coordinates. Five out of seven subjects showed significant activity differences in the visual association region of the left inferior temporal lobe (BA 37, *concrete > abstract*). In two of those subjects, this activated region extended superiorly into the left lateral occipital lobe (BA 19), but it was impossible to determine which area was the primary site of activation due to their close

proximity. No significant activation was detected in primary visual cortex (BA 17) or in the right hemisphere. The authors note that the lateralization cannot be explained simply by the verbal nature of the stimuli since both conditions contained verbal stimuli exclusively. They provide additional discussion of the implications.

Cohen et al.[31] utilized mental rotation of complex objects, a well-studied mental imagery task first described by Shepard and Metzler[32]. On each trial, subjects viewed a pair of perspective drawings of three-dimensional shapes. In a *rotation* task, they mentally rotated one into congruence with the other and determined whether they were identical or mirror images. In the *control* task, objects appeared at the same orientation so the comparison could be completed without mental rotation. Data were analyzed using voxel-wise *t* tests after a comparison between the *t* test and the KS statistic[15] yielded higher significance estimates for the former. In the comparison of *rotation* versus *control*, all subjects showed elevated activity in BAs 7a and 7b (sometimes spreading into BA 40); 88% had activation in the middle frontal gyrus (BA 8); 75% had activation in extrastriate visual cortex, especially BAs 39 and 19 consistent with the location of hMT; 50% had activation in BA 18. In addition, half of the subjects showed activation in frontal, premotor, and hand somatosensory cortex. There was little evidence for lateralization in this study.

These data support the general idea that mental imagery activates the same, or similar, neural machinery as direct visual perception[31]. In mental rotation of complex objects, that machinery necessarily involves areas responsible for tracking moving objects (hMT) and encoding spatial relations (BA 18)[31]. In visualization of spoken objects, it involved a visual association area which encodes complex visual objects (BA 37)[30]. Expectably, that area was not activated in the mental rotation study because complex objects were presented in both conditions.

4. Conclusions

Powerful arguments for the use of fMRI in vision science are the need for (1) high spatial resolution, (2) functional localization, and (3) multiple task conditions in the same subject. By its nature, fMRI has a slight spatial resolution advantage over PET and a sizeable advantage over MEG, although MEG has much better temporal resolution. The need for functionally localizing visual areas makes the slight advantage into an almost all-or-none situation: Although the location and extent of lower visual areas can be coarsely mapped with PET[8], at the current time only fMRI can produce the finely-resolved borders seen in Sereno et al.'s work[13]. Even selective activation of a particular area, such as motion-sensitive hMT+, is sometimes unfeasible with PET due to limited numbers of conditions, which is ultimately due to legal or ethical radiation exposure limits. This was the problem encountered by Cornette et al.[12] who combined fMRI and PET to complete their motion attention study. With fMRI, the number of conditions is limited only by time and subject fatigue. From these technical points, I conclude that fMRI is an indispensable tool in neuroimaging of the human visual system.

But why do we need neuroimaging at all? Vision science has been conducted for decades with only psychophysics, physiology, and anatomy. From these we can infer a hierarchy of processing modules, from low-level feature-extracting modules to high-level cognitive modules. We can also infer many of their interactions and even locate some them within the primate brain (with electrophysiology). In other words, models of the visual system have been constructed without neuroimaging. But now consider the general hypothesis made in all task dependence studies,

although it is often implicit: The hypothesis is that lower-and higher-level modules interact reciprocally at a low level, possibly in the feature-extracting modules or somewhat higher. How can we test this hypothesis? Psychophysics can establish task-dependent effects (such as priming), but finding their locus is extremely difficult. Electrophysiology can provide some answers, but the hypothesis must be narrowed to a certain area. Neuroimaging, however, can detect activity within the whole brain at one time. That is, the entire hierarchy can be made visible so that any point of interaction between top-down (task-driven) and bottom-up (stimulus-driven) signals can be detected and located. Indeed, all of the reviewed studies detected such activation within visual cortex. This is one example of how vision science can benefit from neuroimaging, of which fMRI is an indispensible part.

References

* indicates a study of task dependence reviewed in this article.

1) D. C. van Essen, C. H. Anderson and D. J. Felleman: Information processing in the primate visual system: an integrated systems perspective. *Science*, **255**, 419-422, 1992.

2) S. Clarke and J. Miklossy: Occipital cortex in man: organization of callosal connections, related myelo- and cytoarchitecture, and putative boundaries of functional visual areas. *Journal of Comparative Neurobiology*, **298**, 188-214, 1990.

3) G. R. Fink, P. W. Halligan, J. C. Marshall, C. D. Frith, R. S. Frackowiak and R. J. Dolan: Where in the brain does visual attention select the forest and the trees? *Nature*, **382**, 626-628, 1996.

4) G. Rees, R. Frackowiak and C. Frith: Two modulatory effects of attention that mediate object categorization in human cortex. *Science*, **275**, 835-838, 1997.

5)* C. Buchel, O. Josephs, G. Rees, R. Turner, C. D. Frith and K. J. Friston: The functional anatomy of attention to visual motion: a functional MRI study. *Brain*, **121**, 1281-1294, 1998.

6) A. M. Treisman and G. Gelade: A feature-integration theory of attention. *Cognitive Psychology*, **12**, 97-136, 1980.

7) J. Talairach and P. Tournoux: *Co-planar stereotaxic atlas of the human brain:*. Thieme Medical Publishers, New York, 1988.

8) M. K. Hasnain, P. T. Fox and M. G. Woldorff: Intersubject variability of functional areas in the human visual cortex. *Human Brain Mapping*, **6**, 301-315, 1998.

9) S. Zeki, J. D. G. Watson, C. J. Lueck, K. J. Friston, C. Kennard and R. S. J. Frackowiak: A direct demonstration of functional specialization in human visual cortex. *Journal of Neuroscience*, **11**, 641-649, 1991.

10) S. Sunaert, S. Van Oostende, P. Van Hecke, G. Marchal and G. A. Orban: Many human dorsal stream regions process motion of random textured patterns (Abstract). *Neuroimage*, **3**, S296, 1996.

11)* M. S. Beauchamp, R. W. Cox and E. A. DeYoe: Graded effects of spatial and featural attention on human area MT and associated motion processing areas. *Journal of Neurophysiology*, **78**, 516-520, 1997.

12)* L. Cornette, P. Dupont, A. Rosier, S Sunaert, P. Van Hecke, J. Michiels, L. Mortelmans and G. A. Orban: Human brain regions involved in direction discrimination. *Journal of Neurophysiology*, **79**, 2749-2765, 1998.

13) M. I. Sereno, A. M. Dale, J. B. Reppas, K. K. Kwong, J. W. Belliveau, T. J. Brady, B. R. Rosen and R. B. H. Tootell: Borders of multiple visual areas in humans revealed by functional magnetic resonance imaging. *Science*, **268**, 889-893, 1995.

14)* P. W. R. Woodruff, R. R. Benson, P. A. Bandettini, K. K. Kwong, R. J. Howard, T. Talavage, J. Belliveau and B. R. Rosen: Modulation of auditory and visual cortex by selective attention is modality-dependent. *NeuroReport*, **7**, 1909-1913, 1996.

15) A. Stuart and J. K. Ord: Kendall's advanced theory of statistics, 5th ed. Edward Arnold, London, 1991.

16)* B. A. Haug, J. Baudewig and W. Paulus: Selective activation of human cortical area V5A by a rotating visual stimulus in fMRI; implication of attentional mechanisms. *NeuroReport*, **9**, 611-614, 1998.

17)* M. Corbetta, F. M. Miezin, S. Dobmeyer, G. L. Shulman and S. E. Petersen: Selective and divided attention during visual discriminations of shape, color, and speed: functional anatomy by positron emission tomography. *Journal of Neuroscience*, **11**, 2383-2402, 1991.

18)* T. H. Le, J. V. Pardo and X. Hu: 4 T-fMRI study of non-spatial shifting of selective attention: cerebellar and parietal contributions. *Journal of Neurophysiology,* **79**, 1535-1548, 1998.

19)* G. A. Orban, P. Dupont, R. Vogels, G. Bormans and L. Mortelmans: Human brain activity related to orientation discrimination tasks. *European Journal of Neuroscience,* **9**, 246-259, 1997.

20) K. J. Friston, A. P. Holmes, J. B. Poline, P. J. Grasby, S. C. Williams and R. S. Frackowiak: Analysis of fMRI time-series revisited. *Neuroimage,* **2**, 45-53, 1995.

21) E. A. DeYoe, G. J. Carman, P. Bandettini, S. Glickman, J. Wieser and R. Cox: Mapping striate and extrastriate visual areas in human visual cortex. *Proceedings of the National Academy of Sciences USA,* **93**, 2382-2386, 1996.

22) R. B. H. Tootell, J. D. Mendolla, N. K. Hadjikhani, P. J. Ledden, A. K. Liu and J. B. Reppas: Functional analysis of V3A and related areas in human visual cortex. *Journal of Neuroscience,* **17**, 7060-7078, 1997.

23)* K. M. O'Craven, B. R. Rosen, K. K. Kwong, A.Triesman and R. L. Savoy: Voluntary attention modulates fMRI activity in human MT-MST. *Neuron,* **18**, 591-598, 1997.

24)* T. Watanabe, A. M. Harner, S. Miyauchi, Y. Sasaki, M. Nielsen, D. Palomo and I. Mukai: Task-dependent influences of attention on the activation of human primary visual cortex. *Proceedings of the National Academy of Sciences USA,* **95**, 11489-11492, 1998.

25) S. A. Engel, D. E. Rumelhart, B. A. Wandell, A. T. Lee, G. H. Glover, E. J. Chichilnisky and M. N. Shadlen: fMRI of human visual cortex. *Nature,* **369**, 525, 1994 [published erratum appears in *Nature,* **370**, 106, 1994].

26) T. Watanabe, Y. Sasaki, S. Miyauchi, B. Puetz, N. Fujimaki, M. Nielsen, R. Takino and S. Miyakawa: Attention-regulated activity in human primary visual cortex. *Journal of Neurophysiology,* **79**, 2218-2221, 1998.

27) S. Treue and J. H. Maunsell: Attentional modulation of visual motion processing in cortical areas MT and MST. *Nature,* **382**, 539-541, 1996.

28)* S. P. Gandhi, D. J. Heeger and G. M. Boynton: Spatial attention in human primary visual cortex (Abstract). *Investigative Opthalmology and Visual Science,* **39**, S1130, 1998.

29)* E. Wojciulik, N. Kanwisher and J. Driver: Covert attention modulates face-specific activity in the human fusiform gyrus: fMRI study. *Journal of Neurophysiology,* **79**, 1574-1578, 1998.

30)* M. D'Esposito, J. A. Detre, G. K. Aguirre, M. Stallcup, D. C. Alsop, L. J. Tippet and M. J. Farrah: A functional MRI study of mental image generation. *Neuropsychologia,* **35**, 725-730, 1997.

31)* M. S. Cohen, S. M. Kosslyn, H. C. Breiter, G. J. DiGirolamo, W. L. Thompson, A. K. Anderson, S. Y. Bookheimer, B. R. Rosen and J. W. Belliveau: Changes in cortical activity during mental rotation: a mapping study using functional MRI. *Brain,* **119**, 89-100, 1996.

32) R. N. Shepard and J. Metzler: Mental rotation of three-dimensional objects. *Science,* **171**, 701-703, 1971.