

fMRI adaptation: a tool for studying visual representations in the primate brain.

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x.1 Adaptation and short-term brain plasticity in high-level object areas.

One of the most fundamental properties of the brain that clearly distinguishes it from artificially constructed computational devices is its ability to continuously update its functional properties based on prior experience. This property, also termed brain "plasticity" is manifested on many levels of organization and at many time scales. In recent years, clear demonstrations of experience-dependent modifications of brain activity in the human visual cortex have been established. Fairly long term changes (on the order of days) were observed after subjects learned to recognize unfamiliar shapes (Gauthier et al., 1999), or when trained to recognize subliminally-presented visual objects (Grill-Spector et al., 2000) and even single presentations of objects (van Turennout et al., 2000). Experience-dependent changes are not only evident on long range time scales lasting days, but also in short times scales in the order of seconds.

A particularly robust phenomenon is repetition-suppression, or adaptation, in which repeated presentation of the same visual stimulus leads to a consistent and gradual reduction in activation within seconds of the occurrence of the first image presentation. This phenomenon was termed fMR-adaptation (fMR-A) (Grill-Spector et al., 1999; Grill-Spector and Malach, 2001), and is also referred to as repetition-suppression or repetition-priming (Buckner and Koutstaal, 1998; Koutstaal et al., 2001; Vuilleumier et al., 2002). Similar stimulus-specific repetition-suppression (or mnemonic filtering) has been found in physiological recordings in macaque IT cortex (Miller et al., 1991, 1993).

Visual adaptation is an ubiquitous phenomenon that has been implicated in many perceptual processes, such as contrast and color adaptation (Hadjikhani et al., 1998; Engel and Furmanski, 2001), as well as tilt (Graham 1972; see Clifford, this volume) and motion

after-effects (Clifford, this volume; Tootell et al., 1995; Culham et al., 2000; Huk et al., 2001). However, much less is known about the neural correlates of the adaptation phenomenon in high-level visual areas.

x.2 What is the source of the activity reduction?

Although of fundamental importance, the neural mechanisms underlying fMRI adaptation are not fully understood. Several mechanisms have been proposed to account for adaptation, such as habituation and priming.

Adaptation may be a manifestation of the basic phenomenon of habituation, in which the system suppresses temporally repetitive stimuli. The behavioral correlate of prolonged habituation is typically reduced sensitivity of the observer for test stimuli which have similar properties as the adapting stimulus. This kind of adaptation has revealed orientation selectivity (Graham, 1972), direction selectivity (Tootell et al., 1995; Culham et al., 2000; Huk et al., 2001), and color opponent mechanisms (Bradley et al., 1988; Webster and Mollon, 1994).

Some researchers (Schacter and Buckner, 1998) have suggested that fMRI adaptation may correspond to the behavioral phenomenon of visual priming in which subjects' performance improves with repeated presentations of a stimulus. Behaviorally, visual priming reflects improved performance both in faster reaction times and higher accuracy. In contrast to habituation, visual priming can be manifested after a single exposure to a stimulus (i.e., the "prime"), and is preserved in time scales ranging from seconds to even a year (Cave, 1997). However, it is rather counterintuitive that a reduced cortical response would be

correlated with improved performance. Two theories on the mechanisms underlying priming have been proposed: priming of selective neurons and inhibition of non-selective neurons.

The first approach proposes that the initial processing of the input may leave a trace or prime on selective neurons that are specifically involved in processing the objects that are presented. As a consequence less neural processing is required in order to generate a response to the repeated presentation of the same object. This reduced neural processing could be manifested in a shorter neural duty cycle; that is, neurons fire robustly, but for a shorter period of time. Indeed physiological studies in the macaque (Ringo, 1996) indicate that early visual responses are not affected by image repetition, and suppression occurs only at later times (beginning 200ms after stimulus onset). Further data suggest that repetition suppression occurs for excitatory but not inhibitory neurons (Sobotka and Ringo, 1994) and is stronger for neurons that respond more vigorously to the first stimulus presentation, suggesting that neurons that are selective to the stimulus are adapted more strongly than non-selective neurons (Miller et al, 1993). Importantly, both the mechanism of priming by shortening the duty cycle of selective neurons and habituation by suppressing responses to temporally repetitive stimuli suggest that the selective neurons involved in the initial processing of the stimulus are the ones that are suppressed. It is still an open question whether habituation after prolonged exposure and priming of selective neurons after a single exposure reflect different mechanisms that operate at different time scales or rather different expressions of a single underlying mechanism.

A different model for improved visual processing which underlies priming has been suggested by Li, Miller & Desimone (1993) and has been considered by others (e.g. Wiggs & Martin, 1998, Henson & Rugg, 2003). This model suggests that improved visual processing

by priming occurs by inhibition of non-selective neurons which are initially activated, whereas the selective neurons remained unchanged and are not suppressed. Thus, image repetition generates a more efficient and sparser representation of the visual stimulus across cortex. This hypothesis suggests that fMRI adaptation reflects the suppression of the irrelevant (non-selective) neurons rather than more efficient processing of the repeated visual stimulus by the selective neurons. However, it is unclear why a sparser representation across cortex as suggested by this model would predict faster visual processing (which is the behavioral signature of priming). Furthermore, there is no evidence from Li, Miller & Desimone's experiments or other studies that the selective neurons are not suppressed and the non-selective neurons are suppressed. On the contrary, most of the data suggest that the suppression is highly specific. Finally, evidence from neuroimaging studies suggests that regions that are selective for objects and particular objects categories (such as faces) are the same regions that show fMRI adaptation (Grill-Spector et al. 1999, Avidan et al. 2002).

In sum, while there are yet many unknowns for the neural mechanisms underlying fMRI adaptation, results from both single unit studies and imaging studies suggest that this phenomenon reflects suppression of neurons involved in the processing of the stimulus, that this suppression is stimulus specific. Thus, fMRI adaptation can be used as an important experimental tool to tag specific neural populations.

X.3 fMRI Adaptation: a tool for investigating properties of neural populations in sub-voxel resolution

One of the limitations of conventional fMRI paradigms that rely on the subtraction of activation between different stimulus types is that they average across neural populations that

may respond homogeneously across stimulus changes or may be differentially tuned to different stimulus attributes. Thus, in most cases, it is impossible to infer the properties of the underlying imaged neural populations. fMRI adaptation paradigms have been recently employed to study the properties of neuronal populations beyond this limited spatial resolution of fMRI. These paradigms capitalize on the reduction of neural responses for stimuli that have been presented for prolonged time or repeatedly (Mueller et al., 1999; Lisberger & Movshon, 1999). A change in a specific stimulus dimension that elicits increased responses (i.e. rebound of activity) identifies neural populations that are tuned to the modified stimulus attributes (Figure 1). fMRI adaptation paradigms have been used in both monkey and human fMRI studies as a sensitive tool that allows us to investigate a) the selectivity of the neural populations and b) the invariance of their responses within the imaged voxels. Adaptation across a change between two stimuli provides evidence for a common neural representation invariant to that change, while recovery from adaptation suggests neural representations selective for specific stimulus properties.

FIGURE 1 – Approximately here

x.4 fMRI adaptation for the study of neuronal selectivity

Recent imaging studies tested whether the neural populations in the early visual areas are tuned to visual features, e.g. orientation, color, direction of motion (Tootell et al., 1998; Engel & Furmanski, 2001; Huk & Heeger 2001; Tolias et al., 2001). For example, after prolonged exposure to the adapting motion direction, observers were tested with the same stimulus in the same or in an orthogonal motion direction. Decreased fMRI responses were

observed in MT when the test stimuli were at the same motion direction as the adapting stimulus. However, recovery from this adaptation effect was observed for stimuli presented at an orthogonal direction. These studies suggest that the neural populations in MT are tuned to direction of motion. Similarly, recent studies have shown stronger adaptation in MT/MST for coherently than transparently moving plaid stimuli. These findings provide evidence that fMRI adaptation responses are linked to the activity of pattern-motion rather than component-motion cells in MT/MST (Huk & Heeger, 2002). Thus, these studies provide evidence that the fMRI signal can reveal neural selectivity consistent with the selectivity established by neurophysiological methods.

Recently, combined monkey (Figure 2) and human (Figure 3) fMRI studies showed that coherent shape perception involves early (retinotopic) and higher (occipitotemporal) visual areas that may integrate local elements to global shapes at different spatial scales (Kourtzi, Tolias, Altmann, Augath, & Logothetis, 2003b). fMRI responses across visual areas to collinear contours vs. random patterns were tested. The collinear patterns consisted of a number of similarly oriented elements embedded into a background of randomly oriented elements, while the random patterns consisted of a field of randomly oriented elements. The collinear patterns yield the perception of a global figure in a randomly textured background and are thought to emerge from a segmentation process relying on the integration of the similarly oriented line-segments into global configurations (Hess & Field, 1999 for review; Kovacs & Julesz, 1993; 1994). In the fMRI adaptation paradigm used, stimulus selectivity was deduced by changes in the course of adaptation to a pattern of randomly oriented elements. Adaptation was observed when the adapting random pattern was followed by an identical test pattern. Recovery from adaptation (rebound) was observed

in early visual areas measured in the monkey (V1, V2/V3) and in both retinotopic and higher occipitotemporal regions measured in the human when the adapting random pattern was followed by a different random or a collinear pattern. More importantly, this rebound effect was stronger for collinear than random patterns. Thus, in contrast to traditional approaches, selectivity for collinear shapes was shown not only in higher visual areas that are implicated in shape processing, but also in early visual areas where selectivity depended on the signal (collinear elements) -to- noise (random background elements) ratio within the receptive field.

Further human fMRI studies (Altmann, Bühlhoff, & Kourtzi, 2003) showed decreased detection performance and fMRI activations when misalignment of the contour elements disturbed the perceptual coherence of the contours. However, grouping of the misaligned contour elements by disparity resulted in increased performance and fMRI activations, suggesting that similar neural mechanisms may underlie grouping of local elements to global shapes by different visual features (orientation or disparity). These studies provide additional evidence for the role of early perceptual organization processes and their interactions with higher stages of visual analysis in unified visual perception. Taken together, these findings provide evidence for common mechanisms in the human and non-human primate brain that are involved in coherent shape perception and bridge the gap between previous monkey electrophysiological and human fMRI findings on the neural processing of shapes.

FIGURES 2 & 3 – Approximately here

Furthermore, recent human fMRI studies have used adaptation to test the selectivity of the responses of neural populations in the Lateral Occipital Complex (LOC), a region in

the lateral occipital cortex extending anterior in the temporal cortex, that has been shown to be involved in shape processing (Kanwisher et al., 1996; Malach et al., 1995). fMRI adaptation was used to test whether the LOC is involved in the processing of object shape independent of low level image features that define the shape (Figure 4; Kourtzi & Kanwisher, 2001). An event-related fMRI adaptation paradigm was employed, in which a pair of consecutively-presented stimuli was presented in each trial that lasted for 3 seconds. These studies showed adaptation in the LOC when the perceived shape was identical but the image contours differed (because occluding bars occurred in front of the shape in one stimulus and behind the shape in the other). In contrast, recovery from adaptation was observed when the contours were identical but the perceived shapes were different (because of a figure-ground reversal). Consistent with these results, adaptation was also shown for grayscale images and line drawings of the same objects (Kourtzi & Kanwisher, 2000) but not for objects that differed in their 3D structure (i.e. convex vs. concave) (Kourtzi et al., 2003a). These results suggest that neural populations in the LOC may not represent simple image features, such as contours, but higher-level shape information and 3D objects independent of image cues (i.e. shading and line contours).

FIGURE 4 – Approximately here

x.5 fMRI adaptation for the study of neuronal invariances

Understanding the representation of objects in the brain is crucial for understanding how object recognition occurs efficiently and rapidly. One of the biggest challenges of the object recognition system is dealing with the variability in the appearance of objects without

losing acuity in discriminating between objects that are similar. Theories of object recognition differ most critically in their prediction about the nature of the representation of objects. Some theories (Biederman. 1987) suggest a 3D object-centered representation, while other theories posit that multiple 2D views of an object span its representation (Poggio & Edelman. 1990; Edelman & Duvdevani-Bar. 1997; Ullman. 1996; Tarr and Bulthoff, 1995, 1998; Tarr et al., 1998).

FIGURE 5 & 6– Approximately here

Using fMRI adaptation we investigated (Grill-Spector et al. 1999) the invariant properties of object representations using a variety of objects (animals, man-made objects, faces), formats (gray-level photos, sketches and line drawings) and transformations (size, position, rotation around the vertical and illumination). To test invariance we measured the extent of fMRI adaptation in the LOC when objects were viewed undergoing only one transformation at a time, and keeping the others constant. We found that different kinds of image transformations produce different levels of adaptation within the LOC (which includes object selective regions LO and the fusiform gyrus. Fig. 5). Adaptation in the fusiform was found to be largely invariant to size and position, but not invariant to the direction of illumination and rotation around the vertical axis. Fig. 6a shows the data obtained for faces, similar results were found for cars (Fig. 6b) and animals (Grill-Spector et al., 1999). This suggests that the representation of objects and faces at least in the level of the fusiform is view-based rather than object-

based. In contrast, LO did not show size or position invariance, although it was adapted by presentation of identical images (Fig. 6).

The fact that the more posterior subdivision of the LOC (LO) was sensitive to size and position changes is consistent with macaque studies suggesting a progression of areas in IT cortex, from TEO or PIT that retains some degree of retinotopy to TE or AIT in which the representations are more invariant (Ito, Tamura, Fujita, & Tanaka. 1995; Gross, Rocha, & Bender. 1972). These neuronal invariances to changes in size and position should be contrasted with the high degree of shape selectivity in LOC revealed by the relative lack of adaptation in the blocks where objects from the same basic category (i.e., cars or faces) were presented under identical viewing conditions. Furthermore, the differential profile of adaptation within LOC sub-regions is also incompatible with a global, non-specific arousal being the source of the fMRI adaptation.

x.6 Interpretation of fMRI adaptation Results

Two points should be considered when interpreting the results of fMRI adaptation. First, the level of adaptation can be measured relative to a minimum of activation corresponding to the adapting state (Figures 2 & 3- rebound index = % signal in a condition/ % signal in adapted condition) or a maximum of activation, corresponding to a non-adapted state (Figure 6). In our experiments, the non adapted state consisted of conditions in which different exemplars within an object category were presented. However, we cannot rule out the possibility that some adaptation did occur even in these presumably "non-adapting" epochs. For example, if there were common features among the different object exemplars used in the non-adapting conditions, these may have

adapted neurons specifically tuned to such repeating features. Thus, conclusions that can be derived from adaptation studies refer only to the *relative* effects exerted by one set of images compared to another. Second, the adaptation effect reflects the overall changes in activity of a very large neuronal population; consequently, it may mask opposite effects that may occur within a smaller neuronal population intermixed within the larger population. For example, one could envision that a small subset of neurons in LOC is invariant to face viewpoint, and shows strong adaptation when faces are rotated; however, this adaptation is masked by a larger, viewpoint sensitive neuronal population - leading to the impression of overall viewpoint sensitivity. Single cell recordings are useful in providing additional information about the nature of view dependent representations and about the percentage of cells manifesting view dependent or invariant properties.

Keeping these cautionary points in mind, one can still make educated hypotheses regarding the representation of objects in high order object areas. Using conventional BOLD imaging, previous fMRI studies reported a similar fMRI signal for different face viewpoints (Kanwisher et al., 1997) implying viewpoint-invariant representation of faces in the fusiform gyrus. However, conventional methods cannot distinguish between voxels containing viewpoint-invariant neurons and voxels containing a mixture of neuronal populations tuned to specific ranges of views. The use of fMRI adaptation enabled us to demonstrate that the representation of faces and objects within the fusiform gyrus is actually sensitive to rotation of these objects (faces and cars). This indicates that the representation of a face, at least at the level of the majority of fusiform neurons, is not

viewpoint-invariant, arguing against a full 3D object-centered representation as proposed by some theories.

One surprising result was that viewing the same object under different directions of illumination resulted in substantial recovery from adaptation. Several models suggest that extraction of illumination could be done by lower visual areas (Lehky & Sejnowski, 1988). Our results suggest that sensitivity to the direction of illumination is retained even in higher levels of the visual hierarchy. While size and position changes are probably compensated for in the level of the fusiform, illumination is not. These results are in line with the reported sensitivity of IT neurons to stimulus shading (Ito, Fujita, Tamura, & Tanaka, 1994) and results from some psychophysical experiments (Tarr, Kersten, & Bulthoff, 1998).

x.7 Summary

In summary, fMRI adaptation has been recently used as a tool for the study of visual representations. This paradigm capitalizes on the logic that repeated or prolonged presentation of the same stimulus results in decreased responses compared to presentation of different stimuli. Used in conjunction with imaging techniques, adaptation is a powerful tool for studying the properties of networks of neurons in the human and non-human primate brain. fMRI adaptation allows us to investigate the selectivity and invariance of the responses of neural populations within the imaged voxels. This is not possible with conventional fMRI paradigms that rely on the subtraction of activation between different stimulus types since they average across neural populations that may respond similarly across stimulus changes or may be differentially tuned to different stimulus attributes. Thus, this paradigm goes beyond

the limited spatial resolution of conventional fMRI paradigms and allows us to test the nature of visual representations at a higher resolution in the primate brain. We summarize studies using fMRI adaptation to test for selective responses to different types of stimuli and investigate the invariant properties of visual representations across early and higher visual areas. Although adaptation is a property of neural responses, the relationship between the adaptation of the BOLD signal and neuronal activity is currently not known. Simultaneous recordings of the BOLD signal and electrophysiological activity during adaptation are likely to provide further insights about the relationship between BOLD and neuronal adaptation.

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Figures

Figure 1

Conventional vs. Adaptation fMRI paradigms I. Conventional imaging experiment: fMRI responses to two stimulus conditions A and B are compared to each other. If different neural subpopulations in the measured voxel encode the two stimuli, it is possible that the strength of the BOLD signal will be the same under these two conditions. Therefore, this conventional imaging experiment may fail to characterize the properties of these neural populations. II. Adaptation experiment: stimulus A is shown for a prolonged time or repeatedly resulting in adaptation of the BOLD signal. If different neural subpopulations encode stimulus A and B then after presentation of stimulus B the signal shows a rebound; that is release from adaptation. III. If the same neural subpopulations encode stimulus A and B, then the responses for stimulus B remain adapted after adaptation to stimulus A.

Figure 2

Monkey fMRI study on collinear shapes (Kourtzi et al., 2003). I. Stimuli rendered by oriented line segments: a. Random Pattern used as the adapting stimulus and b. Collinear Pattern used as the test stimulus. II. Localization of the visual areas in the monkey brain. Three consecutive slices (posterior to anterior) from one subject showing the visual areas (V1, V2/V3) that were selected as regions of interest for the analysis of the adaptation experiment. These regions responded significantly more strongly to a full field rotating polar stimulus than blank stimulation periods. Significance charts indicate the results of t-tests. The arrows point to the activated visual areas the borders of which were identified based on anatomical criteria. Major sulci are labeled: LS: Lunate Sulcus, and STS: superior temporal

sulcus. III. fMRI Adaptation results: An fMRI rebound index (percent signal change in each condition / percent signal change in the Identical (adapted) Random Pattern condition) is plotted. A ratio of 1 (horizontal line) indicates adaptation, whereas a ratio higher than 1 indicates recovery from adaptation compared to the minimum responses (adapted fMRI responses) in the Identical condition. This rebound index is plotted for the responses to the Random-to-Collinear Pattern (solid bars) and to the Different Random Pattern (striped bars) conditions across visual areas. The error bars indicate standard errors on the percent signal change averaged across scans and subjects. Collinearity effects were observed in peripheral V1 and central V2, but not in central V1, where only a small number of collinear elements was within the small size receptive fields, and peripheral V2, where the number of random background elements within the receptive field was possibly larger than the number of collinear elements. These fMRI adaptation results suggest that early visual areas contribute to the integration of local elements to global shapes based on the signal (collinear elements) - to- noise ratio (random background elements) within their receptive field.

Figure 3

Human fMRI study on collinear shapes (Altmann et al., 2003). I. Stimuli rendered by Gabors. Examples of a. the random patterns and b. the collinear patterns used as stimuli. II. Localization of the visual areas in the human brain. Functional activation maps for one subject showing the early retinotopic regions and the LOC (lateral occipital complex). The functional activations are superimposed on flattened cortical surfaces of the right and left hemispheres. The sulci are coded in darker gray than the gyri and the Anterior-Posterior orientation is noted by A and P. Major sulci are labeled: STS: superior temporal sulcus, ITS:

inferior temporal sulcus, OTS: occipitotemporal sulcus, CoS: collateral sulcus. The borders (shown by lines) of the early visual regions (V1, V2, VP, V3, V3a, V4v) were defined with standard retinotopic techniques. The LOC was defined as the set of all contiguous voxels in the ventral occipitotemporal cortex that were activated more strongly ($p < 10^{-4}$) by intact than by scrambled images of objects. The posterior (LO) and anterior regions (pFs) of the LOC were identified based on anatomical criteria. III. fMRI Adaptation results: An fMRI rebound index (percent signal change in each condition / percent signal change in the Identical (adapted) Random Pattern condition) reported for the Random-to-Collinear Pattern (solid black bars) and the Different Random Pattern (striped bars) conditions across visual areas. A ratio of 1 (horizontal line) indicates adaptation. This rebound index is shown for central and peripheral subregions of V1 and V2, posterior (LO) and anterior (pFs) subregions of the LOC. The error bars indicate standard errors on the percent signal change averaged across scans and subjects. Similar to the monkey fMRI adaptation study, collinearity effects were observed in peripheral V1 and central V2 consistent with the signal (collinear elements) -to-noise (random background elements) ratio within their receptive field. Interestingly, the collinearity effects in the LOC, where the large receptive fields encode the whole stimulus that consisted of more background than collinear elements, suggest that neural populations in the LOC encode the perceived global shape rather than local configurations.

Figure 4

Shape Processing in the human LOC (Kourtzi & Kanwisher, 2001). Data averaged across 10 subjects showing fMRI adaptation effects in the LOC, that is decreased responses (% signal change from fixation baseline) for identical images of objects (compared to the responses for

different objects in a trial. I. Adaptation is shown for images that have the same perceived shape but different contours due to occlusion. That is, decreased fMRI responses were observed for the Same Shape compared to the Completely Different condition. II. In contrast, no adaptation is shown for images that when rendered stereoscopically have the same contours but different perceived shape due to figure ground reversal (F indicates the shape perceived as the figure in front of the background for each image). That is, increased fMRI responses were observed for the Same Contours compared to the Identical condition. These fMRI adaptation results suggest that neural populations in the LOC encode the perceived shape of objects rather than their local contours.

Figure 5

Regions that activate to faces more strongly than novel objects, houses, cars and scenes with $p < 10^{-4}$ at the voxel level. Lines indicate visual meridians: blue: horizontal visual meridian; red: upper visual meridian; green: lower visual meridian. Location of MT is indicated in blue. Three main regions show higher activation for faces compared to controls: a region in the fusiform gyrus, a region in LO and a region in the posterior STS.

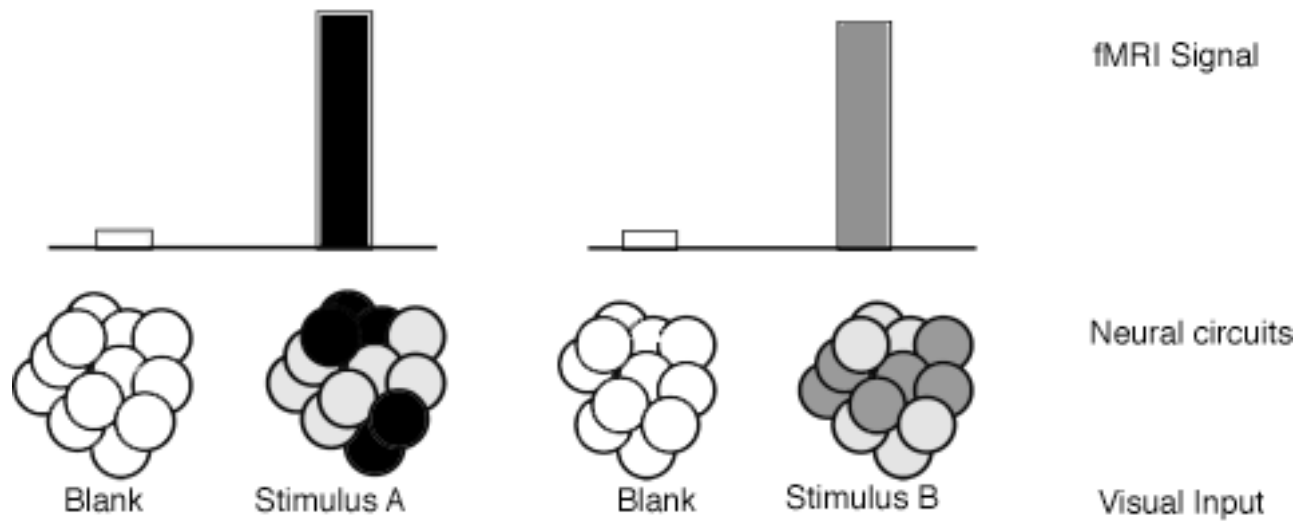
Figure 6

Adaptation ratios across object transformations calculated relative to the non-adapting block of gray-level photographs of different individuals (or objects) taken under the same viewing conditions: $\text{adaptation ratio} = \frac{\% \text{signal}(\text{condition})}{\% \text{signal}(\text{different})}$. A ratio of 1 indicates no adaptation because the activation is the same as for the non adapting stimulus. A ratio less than one indicates adaptation. Asterisks indicate significant adaptation compared to the non-adapting condition. Error bars indicate SEM. Identical:

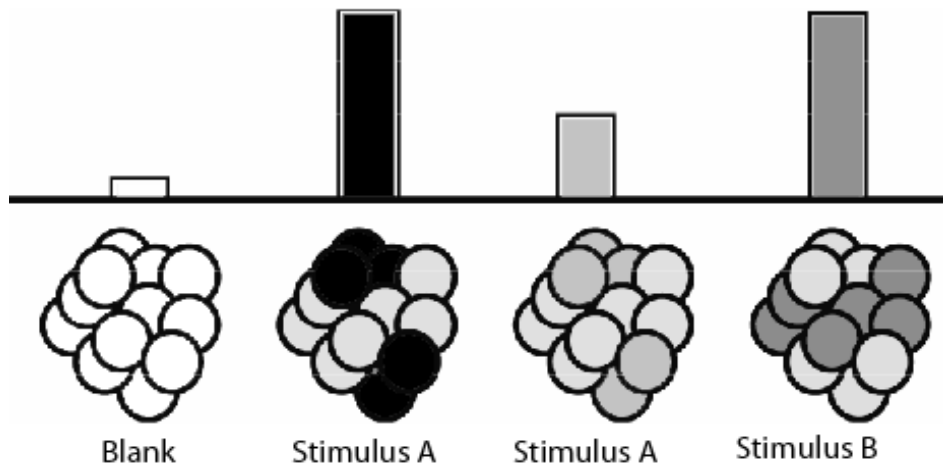
repetitions of the same individual taken under the same viewing conditions. Position: same individual in different positions displaced 6 degrees around fixation. Size: same individual in different sizes (size changes were 3 fold). Illumination: same individual illuminated from 5 different directions. Rotation: same individual in different rotation around the vertical axis ranging from -90° : 90° .

- (a) Adaptation ratios for faces across object transformations in LO and fusiform regions of interest averaged across 14 subjects.
- (b) Adaptation ratios for faces and cars in the fusiform gyrus averaged across 9 subjects.

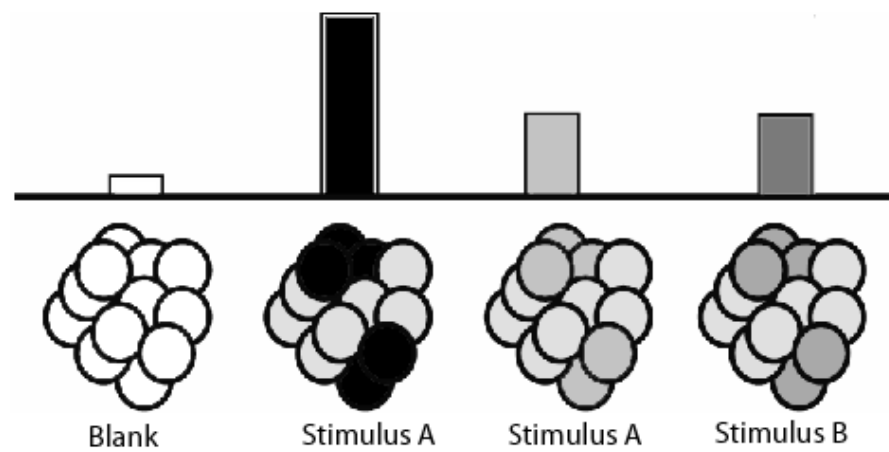
I. Conventional fMRI Experiment



II. fMRI Adaptation Experiment: Selectivity

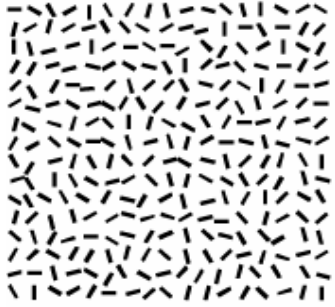


III. fMRI Adaptation Experiment: Invariance

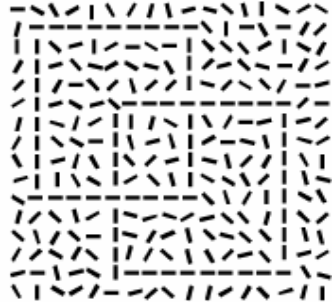


I. Stimuli

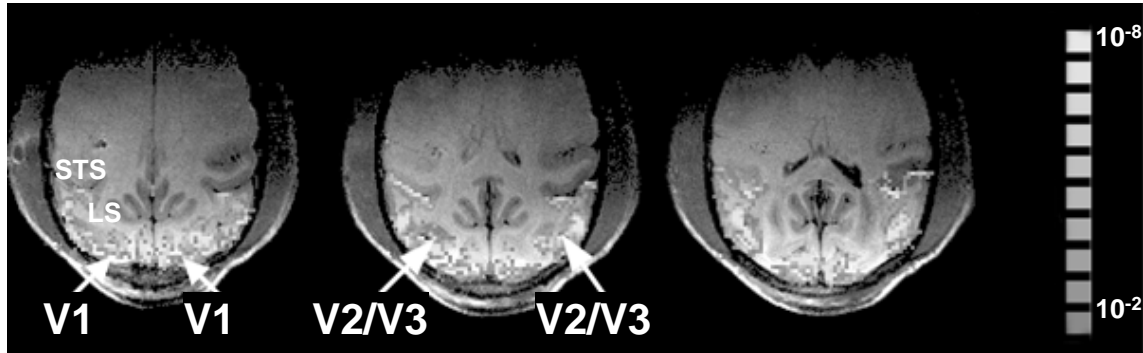
a. Random Patterns



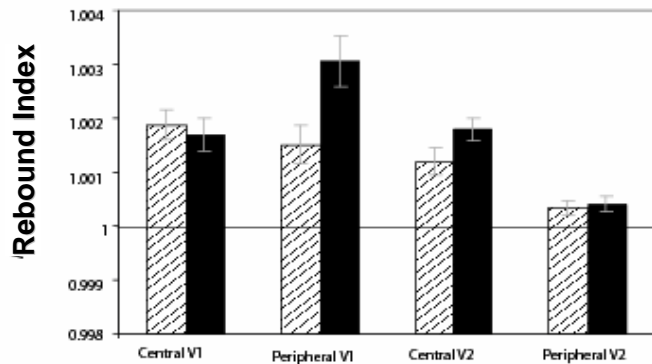
b. Collinear Patterns



II. Regions of interest in the monkey brain

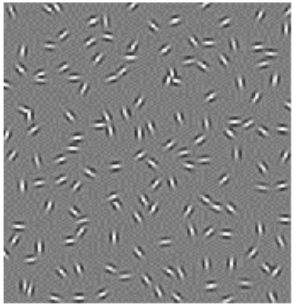


III. fMRI Adaptation

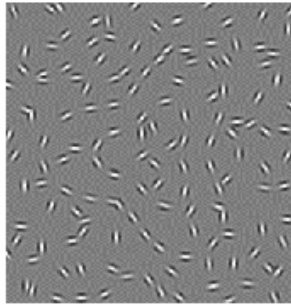


I. Stimuli

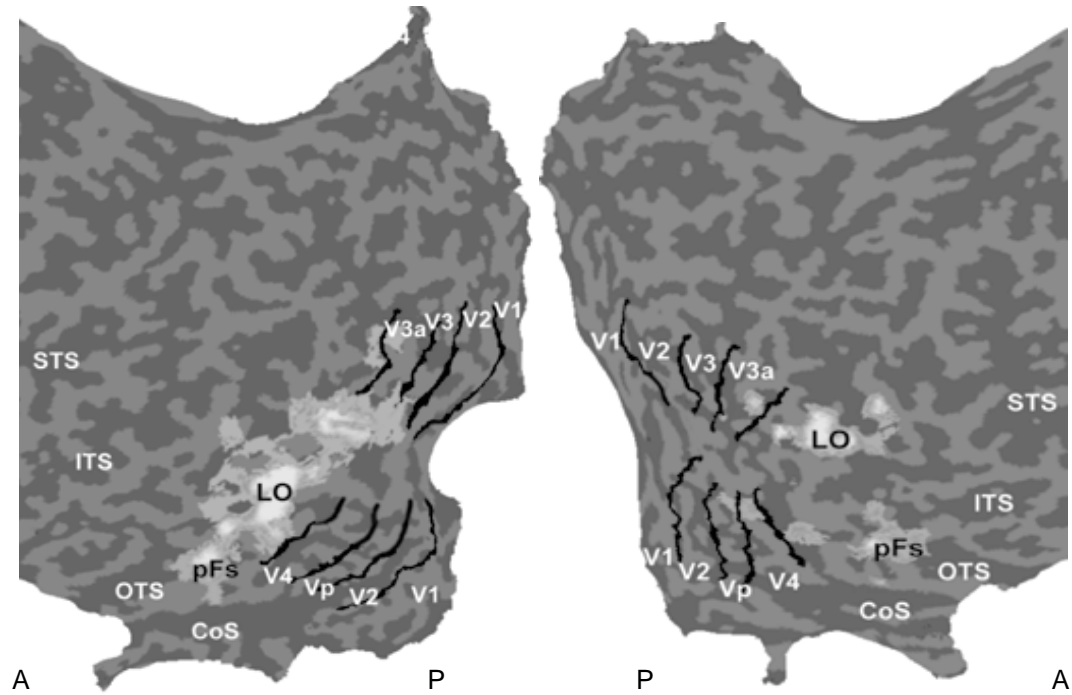
a. Random Patterns



b. Collinear Patterns



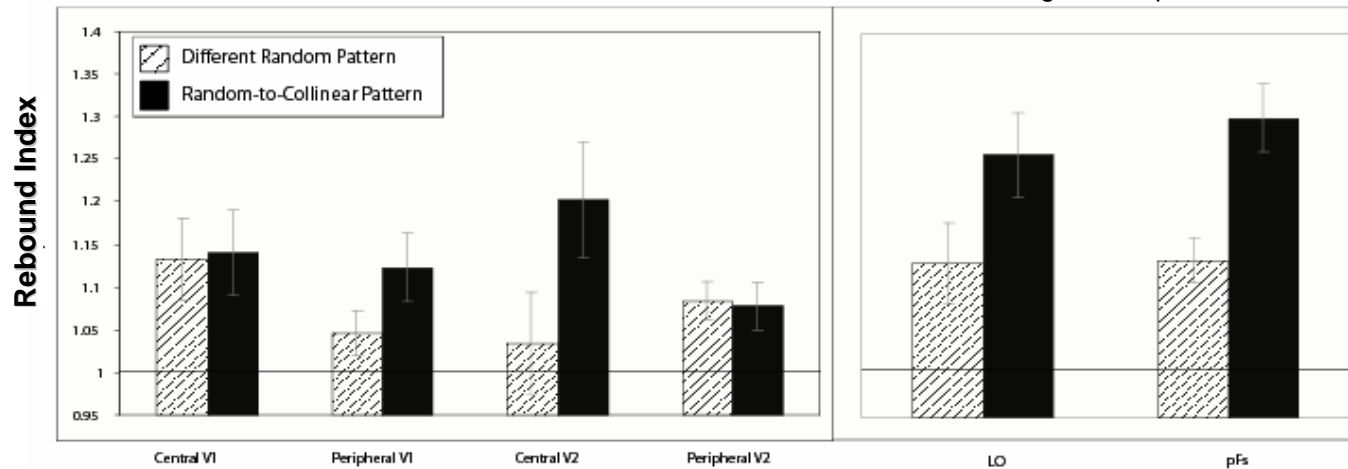
III. Regions of interest in the human brain



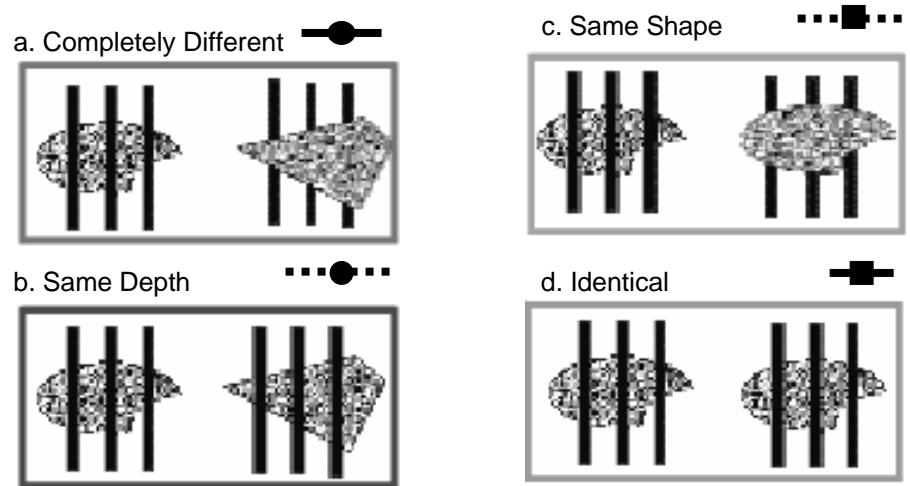
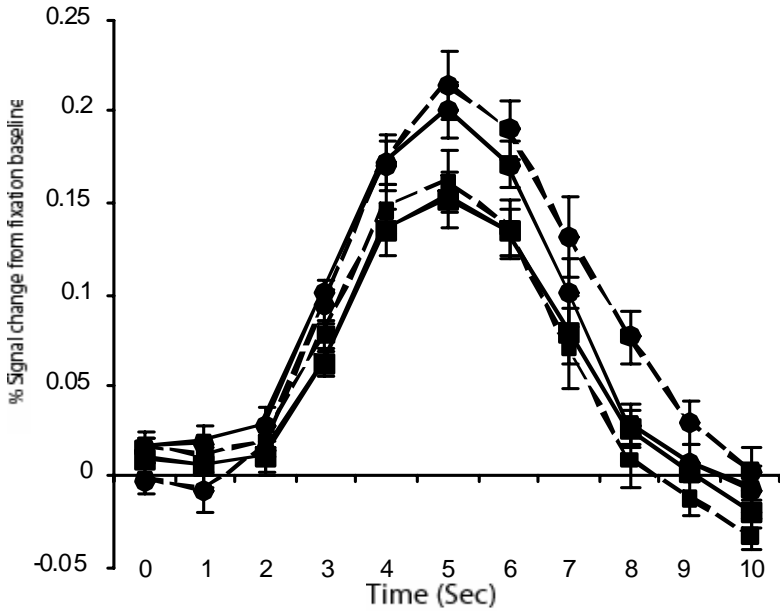
Right hemisphere

Left hemisphere

III. fMRI Adaptation



I. fMRI adaptation in the LOC for the perceived shape



II. No fMRI adaptation in the LOC for local contours

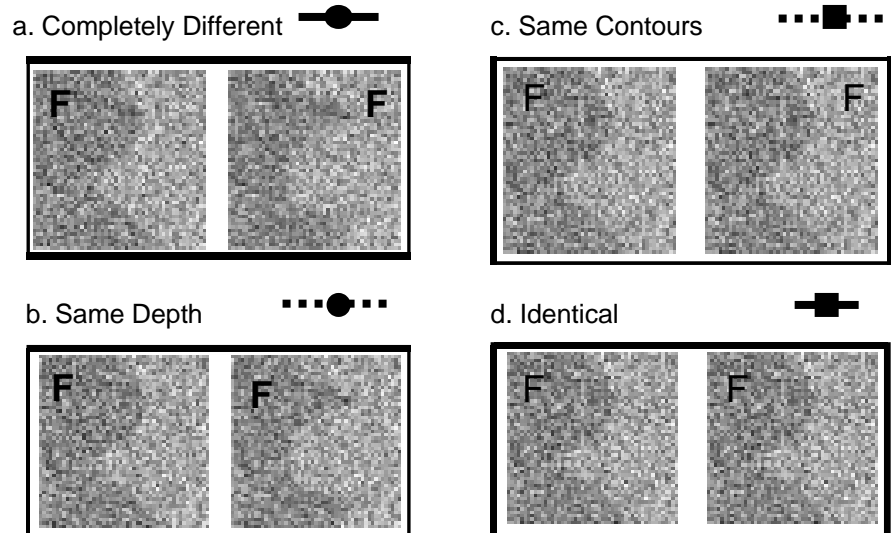
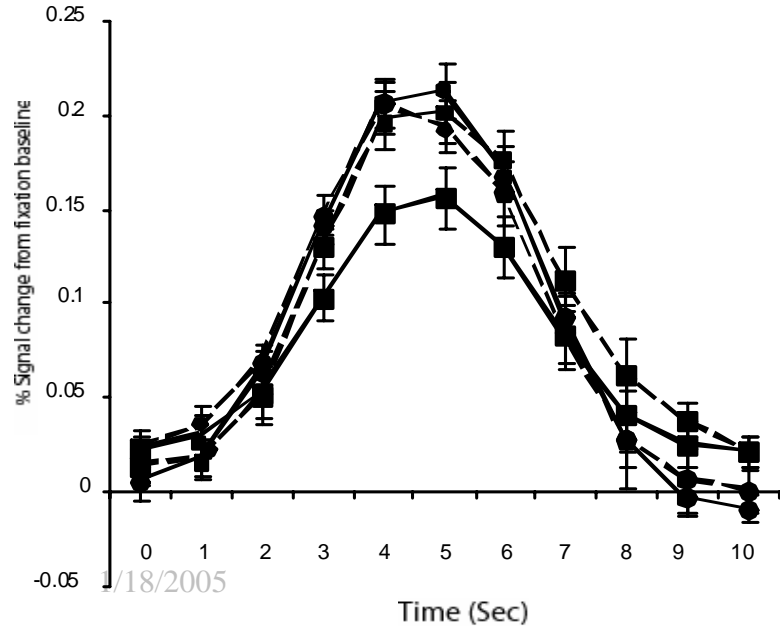
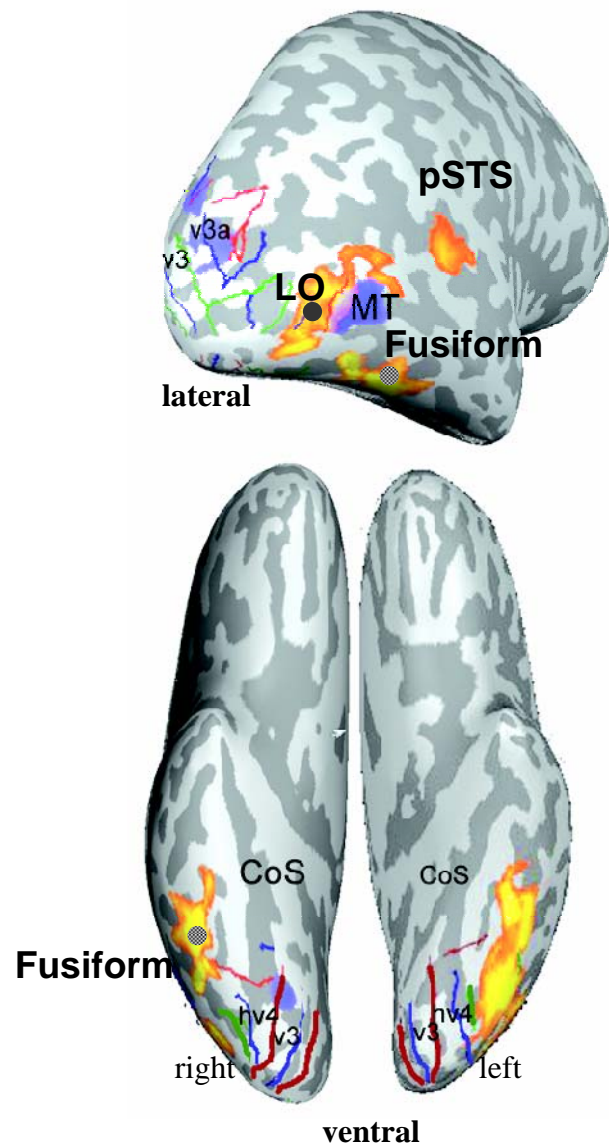
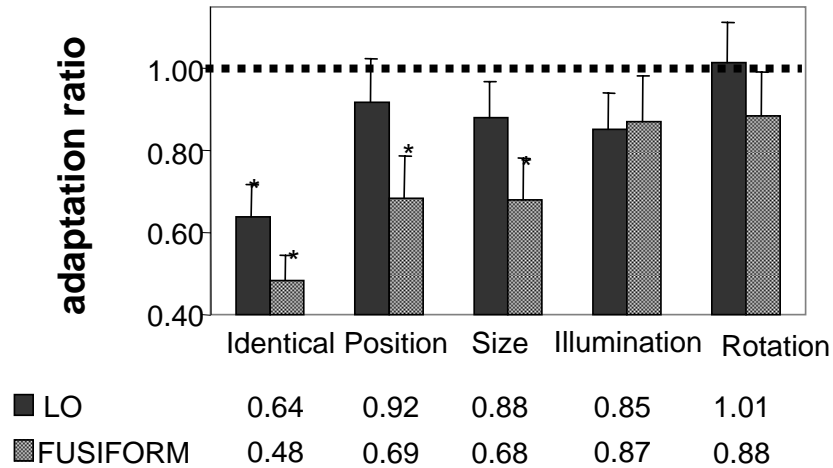


Figure 4



(a) Adaptation for Faces across the LOC



(b) Adaptation for Faces and Cars in the Fusiform

