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Top-down predictions in the cognitive brain

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Abstract

The human brain is not a passive organ simply waiting to be activated by external stimuli. Instead, it is proposed tat the brain continuously employs memory of past experiences to interpret sensory information and predict the immediately relevant future. This review concentrates on visual recognition as the model system for developing and testing ideas about the role and mechanisms of top-down predictions in the brain. We cover relevant behavioral, computational and neural aspects. These ideas are then extended to other domains. The basic elements of this proposal include analogical mapping, associative representations and the generation of predictions. Connections to a host of cognitive processes will be made and implications to several mental disorders will be proposed.

1. Introduction

1.1 A primary function of the brain is to predict its environment

As military tacticians have known for millennia, surprise and uncertainty are costly in terms of time and energy expenditures (Tzu, 2006). Sharing a view expressed in the past, we propose that a fundamental function of the brain is to predict proximate events, which facilitates interactions with external stimuli, conserves effort, and ultimately increases the chances of survival. Useful predictions typically do not arise *de novo*. Even innate abilities of the human brain, such as vision or language, usually require development, during which experience-based mapping of sensory inputs to their identities, and to the appropriate responses, takes place. For example, it is only after years of training that a baseball player is able to effectively anticipate a particular type of pitch, predict the trajectory of the ball by combining top-down information about a particular pitch with bottom-up perception of the rotation and speed of the ball, and correctly decide whether and how to swing at it - all in about half of a second. This ability to rely on stored knowledge and learned modes of behavior reduces the need to consider a large number of potential causes or courses of action, which enables quicker interpretation of endogenous and exogenous events, and faster, more precise, and less effortful responses.

Recent computational and theoretical work demonstrates how predictions can be integrated with sensory input to reduce the computational demands in perception (Engel *et al*., 2001; Grossberg, 1980; Ullman, 1995). However, the neuroanatomical mechanism underlying the generation and efficient representation of predictions in the brain is not completely understood. In this review, we will focus on how the brain generates predictions about the visual world and uses these predictions to allow an efficient and accurate interpretation of the environment.

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Though we largely concentrate on vision, the same general principles can be applied to other sensory modalities, as well as to more complex cognitive domains.

1.2 The efficiency of vision

Picture an impatient driver attempting to overtake a slow-moving vehicle on a busy two-lane road. Much information has to be acquired and computed very quickly by the driver's brain to avoid a collision. The visual system must parse the constantly changing two-dimensional image at the retinae into a coherent 3D representation of the scene, in which the road, the objects on and surrounding it, and the position of the driver's car are accurately identified. The velocities and trajectories of each vehicle in the vicinity must be estimated and changes in these parameters anticipated. Anticipating the movement of other vehicles on the road also involves judging the road conditions, the state of the traffic signals ahead, as well as the other drivers' intentions based on *their* interpretations of these factors and their internal states. Many of these judgments are based not only on visual, but also on auditory, proprioceptive, and even olfactory and social cues (e.g., “will the driver of that junker in front of me emanating noxious smoke and loud music allow me to pass, or try to keep me in the opposite lane?”). Lastly, the forces applied to the car's controls must be computed correctly and adjusted instantly based on both internal (proprioceptive) and external (the vehicle's characteristics and road conditions) parameters. This multimodal information must be analyzed correctly and updated on a moment-to-moment basis to avoid an accident.

Even when we leave aside the other sensory and motor aspects of the task and just concentrate on vision, the complexity of the problem seems immense. The complete understanding of how the brain solves this problem so efficiently remains in many respects elusive, exemplified by our inability to implement anything close to human visual abilities in machine vision. Yet such situations are correctly assessed and successfully navigated every day by millions of drivers with diverse driving abilities, underscoring the nearly universal truth that we are “geniuses at vision” (Hoffman, 1998). We propose that this efficiency of vision arises from the integration of two interacting and cooperating mechanisms – a fast, coarse subsystem that initiates top-down predictions based on partially processed visual input, and a slower, finer subsystem that is guided by the rapidly activated predictions and refines them based on slower-arriving detailed information. Before delving into the details of how predictions may be effected in the brain to facilitate visual processing, we will briefly review the underlying neuroanatomical structure through which visual information flows, and consider how the various pathways process visual information.

1.3 The visual pathways

The primary output from the retina to the lateral geniculate nucleus (LGN) of the thalamus, and from LGN to the primary visual cortex, comprises several parallel pathways with differing information processing characteristics and conduction speeds. The magnocellular (M) pathway has its origin in the large parasol retinal ganglion cells, which collect input from a number of large (diffuse) bipolar cells (Boycott & Wassle, 1991; Kaplan, 2004). The retinal M cells project to the deep (1−2) layers of the LGN, which in turn send projections to layer 4C*a* of the primary visual cortex. The M cells have large receptive fields, high luminance contrast gain, transient and temporally sensitive responses, and fast conduction velocities, but are not color-selective or able to resolve fine details (Kaplan & Shapley, 1986; Merigan & Maunsell, 1993; Schiller *et al.*, 1979; Wiesel & Hubel, 1966). From V1, M neurons project to the thick-stripe regions of V2, continuing to the motion-processing region MT/V5, and then to the higher-order motion and attention regions in the temporal and posterior parietal cortex. The M projections comprise most of the dorsal, or “where”, visual stream, which subserves spatial vision, motion detection, attention, and action planning (Goodale & Milner, 1992; Ungerleider & Mishkin, 1982).

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The second major pathway, the parvocellular (P) pathway, originates with the midget retinal ganglion cells, which typically receive information from just two (ON/OFF-center) bipolar midget cells connected to a single cone (Kaplan, 2004). The P ganglion cells project to the superficial (3−6) layers of the LGN and layers 4A and 4C*b* of V1 (Callaway, 2005; Perry *et al.*, 1984). In part because of their anatomical connections, the P cells have small receptive fields, are color-sensitive, and have low gain for luminance contrast (Kaplan & Shapley, 1986). The latter property renders the P cells ineffective for achromatic stimuli below ~8% contrast (Tootell *et al.*, 1988). The P cells exhibit tonic response properties, low responsiveness to temporal modulation of stimuli, and have low conduction velocities compared with that of the M cells (Kaplan, 2004; Wassle & Boycott, 1991). The P projections form much of the ventral visual ("what") stream (Goodale & Milner, 1992; Ungerleider & Mishkin, 1982), which nonetheless includes some magnocellular inputs (Merigan & Maunsell, 1993). The ventral stream likewise has hierarchical architecture in which visual form information is analyzed in an increasingly complex fashion as it propagates anteriorly, from V1 to V2, V4, and lastly, to the complex form analysis regions in the inferior temporal (IT) cortex. While V1 is sensitive to very basic, local visual properties such as orientation and retinotopic location (Hubel & Wiesel, 1962), neurons in regions in the mid- and anterior IT respond to increasingly larger portions of the visual field and become sensitive to more abstract, viewpoint-, location-, and illumination-invariant properties (Gallant *et al.*, 1996; Qiu & von der Heydt, 2005; Tanaka, 1996, 1997; Vogels *et al.*, 2001). A number of late-stage regions in lateral occipital and inferior temporal regions specialize in recognition of particular classes of visual stimuli, such objects (Bar *et al.*, 2006a; Bar *et al.*, 2001; Grill-Spector *et al.*, 2001; Ishai *et al.*, 2000; Logothetis & Sheinberg, 1996; Malach *et al.*, 1995; Tanaka, 1996), scenes (Aguirre *et al.*, 1998; Epstein & Kanwisher, 1998), and faces (Allison *et al.*, 1994a; Allison *et al.*, 1994b; Kanwisher *et al.*, 1997; Puce *et al.*, 1995).

Less is known about the third, recently discovered, koniocellular (K) visual stream, which originates with the bistratified retinal ganglion cells (Hendry & Yoshioka, 1994). The retinoganglionic K cells terminate between the major (M and P) layers in the LGN, whence geniculate K projections are sent to the "CO blobs" (cytochome oxidase-rich areas) in layers 2−3 of V1. The K cells are vastly outnumbered in both the LGN and V1 by the M and P cells (Callaway, 2005). The K cells appear to have varied spatial resolution, sensitivity to short-wavelength (blue) light, and perhaps higher luminance contrast gain than P cells (Hendry & Yoshioka, 1994; Hendry & Reid, 2000; Norton & Casagrande, 1982). Their conduction velocity appears to be fairly slow, comparable to that of P cells (Hendry & Yoshioka, 1994; Hendry & Reid, 2000; Livingstone & Hubel, 1988; Merigan & Maunsell, 1993). The diverse anatomical and functional characteristics of K cells make it difficult to isolate these cells and to understand their exact role in vision (Kaplan, 2004).

While the M and P projections still remain largely segregated in V1, the dorsal and ventral streams that they form have cross-connections at virtually every level of their processing hierarchies (DeYoe & Van Essen, 1988; Merigan & Maunsell, 1993). This sharing of different types of information presumably allows the integration of the information carried by the different streams into coherent percepts and recognition of stimuli with impoverished color or luminance contrast, albeit more slowly. Attention to the stimulus is thought to be required for this process (Treisman & Gelade, 1980). In addition to the connections between the two cortical visual streams, the cortical regions in each stream have connections with subcortical nuclei, such as the projections from posterior IT (monkey area TEO) to the superior colliculus, and from anterior IT (monkey area TE) to the pulvinar nucleus and the magnocellular division of the mediodorsal nucleus of the thalamus (Webster *et al.*, 1993, 1995).

Much of research in vision has justifiably concentrated on information arriving via the primary visual pathway (i.e., retina-LGN-primary visual cortex) and propagating along the cortical

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visual streams. However, other important visual input and processing routes exist in the brain. Indeed, projections from the retina to structures other than the LGN are hardly insubstantial, with at least nine other targets besides the LGN (Weiskrantz, 1996). Among those alternate input routes, the ones most relevant to facilitating cortical visual analysis may be inputs to the superior colliculus, which projects to the pulvinar nucleus of the thalamus (Diamond & Hall, 1969), as well as a direct retinal input to the pulvinar (Leh *et al.*, 2006). While the exact functions of the pulvinar, the largest visual (and auditory) nucleus in the human thalamus (Grieve *et al.*, 2000), remain poorly understood (Casanova, 2004), it seems to be involved in the processing and relay of partially analyzed information, visual memory, and perhaps auxiliary visual function in the absence of cortical vision (Weiskrantz, 1996). Most of the visual inputs to the pulvinar are from the complex cells in layers 5 and 6 (i.e., feedback) of the primary visual cortex (Abramson & Chalupa, 1985; Casanova, 1993), indicating that it is a higher-order relay and association nucleus involved in processing information that has already undergone an initial analysis in the primary sensory cortex. In addition, the various subdivisions of the pulvinar also have bidirectional connections with many of the cortical regions in both visual streams (Webster et al., 1993, 1995), allowing the pulvinar to integrate information coming from several cortical processing levels and visual field representations (Casanova, 2004). These cortical connections overlap with inputs from the superior colliculus (Benedek *et al.*, 1983). The pulvinar projects to most of the visual association and prefrontal cortices (Giguere & Goldman-Rakic, 1988; Goldman-Rakic & Porrino, 1985; Grieve et al., 2000; Guillery, 1995; Guillery & Sherman, 2002; Romanski *et al.*, 1997). It has been implicated as potentially being involved in supporting residual visual abilities in “blindsight” (Cowey & Stoerig, 1995), a condition in which cortically blind patients have no perception of visual stimuli but retain latent visual abilities that can be used to guide their actions (Sahraie *et al.*, 2006; Weiskrantz, 1996, 2004). The pathways subserving this residual vision system may overlap with the “fast brain” proposed by Bullier (2001a, 2001b) and may be part of a key bypass route from the primary visual cortex to the higher-order regions in the prefrontal cortex (Sherman & Guillery, 2004). We elaborate on these and other possibilities as they relate to our model of top-down facilitation in vision in the following sections.

1.4 Feedforward and feedback views of visual recognition

Visual recognition has been traditionally considered a bottom-up, feedforward process. According to this view, visual information flows from lower-level regions to higher-level regions until recognition is accomplished, after which semantic analysis and/or object name information can be activated, depending on situational demands. This unidirectional view of visual processing has been largely influenced by the ascending hierarchical processing architecture of the ventral visual stream as discussed above. However, due to the noise and clutter in natural images, a purely bottom-up architecture has fundamental difficulties in isolating objects in all but the simplest circumstances (Bullier, 2001a, 2001b), something that was also learned from efforts in computer vision (Sharon *et al.*, 2006; Ullman *et al.*, 2002). For example, given the tremendous variation in lighting, shadows, occlusions, reflections and the like, it is nearly impossible for bottom-up and lateral processes (i.e., those relying only on short-range, horizontal connections) to “know” which edges should be assigned to one shape vs. another, which makes it difficult to unify locally-processed information into a global percept. Moreover, perceptual completion often requires spanning large regions of the visual field and thereby of the primary visual cortex – too distant for the short reach of local inhibitory and excitatory connections (Angelucci & Bullier, 2003). Furthermore, imperceptible or ambiguous properties of a stimulus, such as features that are occluded, cannot be resolved by simply analyzing sensory input. In this case, the nature of the stimulus can only be resolved by inferring the imperceptible or ambiguous properties of the input based on information derived from previous experience (Friston, 2005).

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Consequently, “top-down,” feedback projections from higher-level regions would be necessary to account for our visual abilities in all but the simplest of circumstances (Angelucci *et al.*, 2002a; Angelucci *et al.*, 2002b; Shmuel *et al.*, 2005; S.J. Thorpe & Fabre-Thorpe, 2001). The very nature of the connections between visual regions makes it highly unlikely that only forward processing would be employed in analyzing visual input. The majority of the connections between LGN, V1, and V2, as well as V3, V4, IT and other extrastriate cortical regions are bidirectional (Ergenzinger *et al.*, 1998; Felleman & Van Essen, 1991; Ghashghaei *et al.*, 2007; Lund *et al.*, 1993; Pandya, 1995; Rockland & Drash, 1996), and the number of purely feedback connections is estimated to even exceed the number of feedforward inputs (Salin & Bullier, 1995). This supposition is supported by findings showing that basic analysis in the early visual areas is influenced by more-global projections from the higher levels (Porrino *et al.*, 1981). Even at the lowest cortical processing levels, which have small receptive fields, inactivation of feedback connections to V1 lead to weakened suppression of surrounds in center-surround cells (Angelucci & Bullier, 2003), and feedback connections from V2 seem to shape simple sensitivities in V1 (Shmuel et al., 2005). In addition, under certain viewing conditions, neurons in V1 can react to stimuli outside of what is thought to be their traditional receptive fields (Kapadia *et al.*, 1995) and select neurons in V2 are sensitive to surround stimulation when the surround stimulus has an eccentricity as large as ten times the size of these neurons' classic receptive fields (Zhang *et al.*, 2005), indicating top-down feedback. Furthermore, varying attentional modulation has been shown to modulate the neural responses as early as in the primary visual cortex (Somers *et al.*, 1999). It seems clear that a full understanding of visual processing cannot be achieved until we understand the role and functional properties of the top-down, feedback processes in the brain.

1.5. Anatomical and functional differences between top-down and bottom-up connections

The differences between the feedforward and feedback connections in the visual processing hierarchy have helped to shape our thinking about the role of bottom-up and top-down processes. (For the purposes of this review, we consider feedforward projections to be bottom-up, and feedback projections to be top-down.) In particular, connections from lower-level regions tend to project to relatively few regions higher in the processing hierarchy, the projections within these regions are relatively focused, and these feedforward projections tend to terminate in the superficial layers of the cortex. In contrast, projections that originate in higher-level regions tend to target many regions in the processing hierarchy, have wider connections patterns within these regions, and terminate predominantly in the deep cortical layers (Angelucci et al., 2002a; Angelucci et al., 2002b). For example, the top-down projection from V5 to V2 is more widely distributed than the focused bottom-up projection from V2 to V5 (Shipp & Zeki, 1989). Additionally, V1 receives feedback projections from a greater number of regions than the number of regions to which it sends ascending projections; e.g., V1 receives top-down projections from IT while sending no direct bottom-up projections to IT (Barone *et al.*, 2000; Boussaoud *et al.*, 1990; Livingstone & Hubel, 1987; Lund *et al.*, 1975; Perkel *et al.*, 1986; Rockland & Van Hoesen, 1994; Shipp & Zeki, 1989; Suzuki & Eichenbaum, 2000; Ungerleider & Desimone, 1986a, 1986b). These asymmetries in the properties of top-down and bottom-up connections suggest an important distinction in the role of feedforward and feedback projections. Because feedforward projections are more focused and restricted, bottom-up processing tends to exhibit a structured build-up of information from simple to complex, with activity from lower regions in the processing hierarchy driving activity in the higher regions. In contrast, due to the more diffuse and dispersed nature of feedback projections, top-down processes coordinate and bias local activity across lower-level regions based on information derived from global, contextual, and gist information.

These differences in the connectivity patterns of top-down and bottom-up projections are reflected by asymmetries in their function. In particular, while bottom-up projections are

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driving inputs (i.e., they always elicit a response from target regions), top-down inputs are more often *modulatory* (i.e., they can exert subtler influence on the response properties in target areas), although they can also be driving (Buchel & Friston, 1997; Girard & Bullier, 1989; Sandell & Schiller, 1982; Sherman & Guillery, 2004). Top-down input probably has to be at least partly modulatory, as purely driving feedback could induce neural activity in lower-lever regions that would be indistinguishable from that in response to external stimuli (Adams & Rutkin, 1970; Moriarity *et al.*, 2001; Nashold & Wilson, 1970; Vignal *et al.*, 2007). This could give rise to hallucinations (Siegel *et al.*, 2000). While it may be beneficial to sensitize one's neural representations of a stove, sink, and a refrigerator when walking into a kitchen to aid in the recognition of these objects, it would be counterproductive to “perceive” (i.e., hallucinate) those objects without any sensory input from the environment. The tendency of feedforward and feedback projections to terminate in different cortical layers (deep versus superficial) (Bernardo *et al.*, 1990; Garraghty *et al.*, 1989; Jones, 1986; Schroeder *et al.*, 1995) may help in segregating top-down and bottom-up inputs to prevent “network hallucinations”.

1.6 Theoretical and computational models

A number of theories have described the computational processes that may be employed by top-down mechanisms to facilitate sensory processing (Friston, 2005; Grossberg, 1980; Hinton *et al.*, 1995; Mumford, 1992; Ullman, 1995). These models, taking into account the functional and structural properties of feedforward and feedback connections described above, generally posit that predictions based on prior experience are generated in higher-level areas and projected to lower-level areas to guide the recognition process driven by sensory information. Guidance is implemented by using these top-down predictions to sensitize bottom-up stimulus-driven processing. Therefore, top-down predictions facilitate the recognition process by reducing the number of candidate representations of an object that need to be considered. For example, when trying to identify a stove in a kitchen, prior experience with kitchens may be used to predict that the most likely identity of the square object standing on the floor is a stove or a dishwasher, which eliminates the need to consider a large number of possible object identities.

But what happens when a top-down prediction does not fully match the bottom-up representation? For example, what transpires in the brain when the square object on the floor of the kitchen is actually a television, when the prediction is that the most likely identity of the object is a stove or dishwasher? Many models posit that top-down and bottom-up information might be integrated via an iterative error-minimization mechanism, with information processed in recursive, interacting loops of activity (Friston, 2005; Grossberg, 1980; Hinton et al., 1995; Mumford, 1992; Ullman, 1995). Specifically, the prediction sent from higher-level regions would be matched with stimulus-generated bottom-up activity, and an error signal is generated reflecting any mismatch between the predicted signal and the actual stimulus-generated activity. If the error signal is substantial, the mismatch is projected to the higher neural region where a new prediction, refined by the error signal, is generated. When the perceptual task is simple, such as identifying clearly presented, commonly encountered stimuli, the initial prediction or set of predictions is likely to match up well with the sensory input, rendering multiple iterations of this cycle unnecessary. However, if the identity of the object has not been resolved in the initial pass, the cycle of matching and refining predictions continues until the identity of the input stimulus has been determined. While these models (Friston, 2005; Grossberg, 1980; Hinton et al., 1995; Mumford, 1992; Ullman, 1995) generally fit into the qualitative framework described above, their underlying mathematical, computational, and proposed cortical mechanisms differ in their details. Below we concentrate on elucidating some of the differences between them.

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In the adaptive resonance theory (ART) of Grossberg (1980), the matching between top-down and bottom-up information is accomplished through a pattern-matching algorithm that leads to a stable and efficient representation of the input identity. The prediction patterns that match the sensory-based representations lead to an amplification of the matching neural signal. Conversely, mismatches lead to an extinction of the signal and alert the system that a new pattern must be generated. This new prediction pattern is a combination of the parts of the initial prediction that matched the stimulus features and updated features that improve the fit with the stimulus-driven information (Grossberg, 1980).

Mumford (1992) proposed a mechanism based on an architecture of multiple local top-down/bottom-up loops that traverse adjacent levels in the processing hierarchy. These loops carry both the information that has been successfully predicted by higher-level regions and the residual that needs to be explained in further iterations of the loop or at other levels of the processing hierarchy. In this model, the top-down/bottom-up loops are used both for lower-level visual processes, such as segmentation (e.g. between the level that attempts to segment the input image based on local-feature properties, and the next-higher level that generates predictions about how the larger image should be segmented), and for higher-level processing, such as determining the conjunction between objects. These loops are relatively restricted in how much of the processing network they transverse, like links on a chain, therefore this model posits that processing builds up in increasing complexity. However, in contrast to bottom-up models, the build-up of processing takes into account information based on prior experience in its top-down/bottom-up loops. These loops demonstrate the type of neural architecture necessary for the integration of top-down and bottom-up information. Mumford's model has been extended with statistical methods (e.g., Kalman filtering, 1960) for addressing various questions such as how receptive fields develop (Rao & Ballard, 1997).

The “counter streams” framework of Ullman (1995) proposes a large-scale bidirectional information flow in which sensory input triggers parallel bottom-up and top-down processing streams. These streams simultaneously activate multiple candidate interpretations of the information coming from the senses, leading to rapid and flexible processing. Recognition is accomplished when a match is found and the top-down and bottom-up “counter streams” meet. This model contrasts with Mumford's model (1992) in that the top-down and bottom-up streams transverse multiple regions and levels of the processing hierarchy. Thus, Ullman's model posits that different levels of the processing hierarchy are able influence one another.

Recent work by Friston (2005) employs an empirical Bayesian statistical framework to describe how predictions can guide the recognition process. This framework is largely complementary to Mumford's work in that it assumes the architecture of top-down/bottom-up loops between adjacent levels of the processing hierarchy. Friston employs a Bayesian statistical framework with the explicit underlying assumption that experience-based information is used to minimize prediction error when processing sensory information. The iterative refining process alters the parameters in the model through Hebbian-like changes in cortical plasticity. According to Friston (2005), experience with a stimulus alters the weights of the top-down and bottom-up connections to reflect the refined representation that results from minimizing prediction error. This learning scheme is able to account for several cognitive phenomena, such as mismatch negativity and priming-related neural response reductions.

1.7 The role of neural synchrony in top-down/bottom-up interactions

A common feature of the frameworks that support a critical role for top-down influences is the need for a mechanism for matching information in top-down and bottom-up processing streams. Typically, these models, as well as other experimental and theoretical work, suggest that the mechanism by which this matching is accomplished is the precise synchrony of the

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pattern of neural activity across the processing hierarchy (Bar et al., 2006a; Engel et al., 2001; Friston, 2005; Grossberg, 1980; Mumford, 1992; Siegel et al., 2000; Ullman, 1995).

Synchrony between neural activity has been hypothesized to be a signature of integration of neural processing both in local processing, such as for binding local stimulus features, and across disparate neural regions, such as for integrating across modalities or exchanging information across the brain (Engel et al., 2001; Hummel & Biederman, 1992; Simoes *et al.*, 2003; Tononi *et al.*, 1992; Varela *et al.*, 2001)[1]. In the case of top-down/bottom-up integration, synchronized activity may represent the match between higher-level and lower-level representations of the stimulus while the unsynchronized activity would reflect any residual mismatch, or "error", in the representations. Therefore, the iterative process of refining the representation until a sufficient representation of the stimulus has been achieved can be described as the process by which the neural activity in higher- and lower-level regions is refined until the patterns of activity between these regions synchronize. For example, in Ullman's "counter streams" model, when the top-down and bottom-up streams "meet" to achieve recognition it might be reflected in increased synchrony of the activity in higher and lower level regions (Ullman, 1995). Recent results support this view, demonstrating that neural synchrony increases with an improved match between top-down and bottom-up processes (Bar et al., 2006a; Ghuman *et al.*, 2006; von Stein *et al.*, 2000; von Stein & Satnthein, 2000).

A recent computational model demonstrates a physiologically plausible mechanism describing how synchronized activity may govern top-down/bottom-up integration, and how this interaction can facilitate cortical processing (Siegel et al., 2000). In this computational study, the authors simulated a hierarchical neural network with separate top-down and bottom-up connections and inputs based on empirical *in vivo* and *in vitro* findings. A Poisson spike train with added noise was used to simulate naturalistic stimulus input. The key result was that top-down input reduced the noise in the representation of the stimulus compared with bottom-up processing alone. Furthermore, as the match between higher- and lower-level representations improved, the synchrony between the activity in them increased. Additionally, increased synchrony between the activity in higher- and lower-level regions (i.e. when the representations matched) decreased the noise of the neural representation of the stimulus far more than non-synchronized (i.e. non-matching) top-down projections. Moreover, increasing the strength of the top-down signal, particularly if the activity in the higher- and lower-level regions synchronizes, not only leads to less-noisy representations, but also to faster processing. Additionally, the authors also demonstrated how, with two bottom-up inputs (representing two competing stimuli), top-down influences can strengthen processing of one stimulus over another, e.g. in response to contextual or attentional biases (Desimone & Duncan, 1995). This model demonstrates how top-down/bottom-up synchrony could lead to facilitated and biased processing as typically observed with priming and cueing paradigms (Brunia, 1993; Buckner *et al.*, 1998; Dale, 2000; Desimone, 1996; Grill-Spector *et al.*, 2006; Jennings & van der Molen, 2005; Wiggs & Martin, 1998; Zago *et al.*, 2005). Indeed, a recent study demonstrates increased synchrony between higher- and lower-level neural regions with facilitated processing in repetition priming (Ghuman *et al.*, In prep-a).

Finally, in this computational model, due to the physiological differences between the different inhibitory inputs, synchrony between higher- and lower-level regions occurred specifically in the lower frequency bands when top-down influences were present. The lower-frequency-band synchrony for top-down interactions is consistent with differences in the temporal properties of the receptors in the cortical layers where feedforward and feedback projections terminate. Specifically, feedforward projections are mediated through fast GABA-A and AMPA

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[1] Although "synchrony", strictly speaking, applies only to coupled activity with zero phase difference, here it will refer to phase-locked activity with any phase lag, as a general term indicating coupling between neural signals.

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receptors, while feedback projections are mediated by slower GABA-B and NMDA receptors (Salin & Bullier, 1995). Removing the top-down influence in this model suppressed the lower-frequency synchrony and increased higher-frequency synchrony. This result is consistent with experimental results demonstrating increased cross-cortical synchrony in the lower theta-, alpha-, and beta-frequency bands when top-down influences are greater (Bar et al., 2006a; von Stein & Satnthein, 2000) and greater local synchrony in the higher, gamma-frequency bands, when bottom-up processing predominates (Engel et al., 2001; Tallon-Baudry & Bertrad, 1999; von Stein et al., 2000; von Stein & Satnthein, 2000). Additionally, theoretical considerations suggest that the slower temporal dynamics of feedback projections are more appropriate for top-down effects, which tend to be modulatory and prolonged, than for more-transient sensory evoked responses (Friston, 2005). In particular, top-down information, such as the global and context information, is useful for facilitation during the entire processing sequence and can aid multiple processing levels. On the other hand, it is wasteful to maintain the representation of bottom-up information once a more complete representation has been formed. For example, once the identity of an object has been found, it would be inefficient to continue to represent every detail about the object, because many of these details are insignificant (Wiggs & Martin, 1998; Zago et al., 2005).

In summary, an improved match between higher- and lower-level representations can result in improved synchrony in lower frequency bands and facilitated processing, demonstrating how top-down influences can improve processing on a neural level. It is important to note that with small modifications to the assumptions about the underlying neural architecture of this work by Siegel et al. (2000), it could be adapted to fit with the various theoretical frameworks of top-down/bottom-up interactions described above. For example, if the higher-level and lower-level regions in the model are assumed to be in adjacent regions along the hierarchy, this model can describe a computational example of how Mumford's (1992) mechanism may be implemented. On the other hand, this model also fits with Ullman's “counter-streams” mechanism (1995) in that the top-down and bottom-up signals are mapped onto separate but interacting neuronal populations. Additionally, if the computations underlying top-down/bottom-up processing fit the assumptions of prediction error minimization and empirical Bayesian statistics, this model could be adjusted in accordance with Friston's framework (2005). Finally, if these computations adapted the complex pattern-matching algorithm in the ART framework, this computational work could be implemented in Grossberg's framework (1980).

2. Evidence for top-down facilitation in visual recognition

2.1 A model for the triggering of top-down facilitation in object recognition

The theoretical treatments described above provide a framework for the computations that may be involved in top-down/bottom-up interactions in visual recognition. However, they do not specify what information may be used to initiate top-down predictions, which neural regions would be involved, and how information travels through the brain during top-down facilitation of object recognition. A recent proposal by Bar (2003), building on early top-down/bottom-up models (Grossberg, 1980; Kosslyn, 1994; Mumford, 1992; Ullman, 1995) and recent findings (Bar et al., 2001), described a neural and cognitive mechanism of how top-down predictions might be initiated and employed to facilitate object recognition. According to this top-down facilitation model, a coarse, partially processed version of visual afferents is rapidly projected from the early visual regions to the orbitofrontal cortex (OFC), a key multimodal association region (Barbas, 2000; Kringelbach & Rolls, 2004). The top-down facilitation model proposes that the rapidly processed information is projected through the magnocellular pathway, based on the rapid conduction velocities of this pathway (Bullier & Nowak, 1995; Merigan & Maunsell, 1993; Shapley, 1990). As described in Section 1.3, the M pathway is particularly well-attuned to low-spatial-frequency (LSF) visual information; therefore the model predicts

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that the partially processed visual information projected to OFC primarily contains LSFs. OFC selects potential matches based on the global, LSF-based properties of the visual input. Predictions about the candidate objects from which the particular LSF image might have arisen are then projected to the object recognition regions in IT. Bar (2003) hypothesized that top-down predictions bias the output of the bottom-up visual analysis and facilitate the search by providing global constraints on the possible interpretations of the bottom-up outputs. This would reduce the number of candidate objects that need to be considered to identify the stimulus, enhancing the speed and accuracy of recognition (Figure 1).

With respect to the origin of this top-down facilitation, several recent findings point to OFC as a probable site where it might be initiated. Located on the ventral surface of the prefrontal cortex, OFC is known to be a multimodal association-processing region (Barbas, 2000; Rolls, 1999a; Rolls, 2004), well suited for integrating high-level information and generating predictions. OFC is extensively connected with the object recognition regions in IT (Cavada *et al.*, 2000; Kringelbach & Rolls, 2004), and is also known to have strong bidirectional connections with the amygdala (Amaral & Price, 1984; Barbas & De Olmos, 1990; Carmichael & Price, 1995). OFC also has reciprocal connections with two major association nuclei of the thalamus: the magnocellular division of the mediodorsal nucleus and the pulvinar (Barbas & De Olmos, 1990; Ongur & Price, 2000; Semendeferi *et al.*, 1997). OFC has been shown to be involved in regulating emotion, assessing potential rewards, decision-making (Freedman *et al.*, 2003), and cognitive control (Bechara *et al.*, 1998; Bechara *et al.*, 1997; Bechara *et al.*, 2000; Tomita *et al.*, 1999). Note that all of these functions involve generating predictions about some internal or external stimulus or process, and exerting influence on limbic, sensory, or motor regions to regulate their output. Importantly, OFC also has been shown to receive and process visual information (Bar et al., 2001; Barbas, 2000; Ongur & Price, 2000; Rolls *et al.*, 2005; Thorpe *et al.*, 1983; Voytko, 1985; Winston *et al.*, 2007). Thus, OFC seems to be well situated for integrating and broadcasting information used for rapid visual processing, as well as for predictions in general (Bar, In press).

2.2 Testing the top-down facilitation model

The top-down facilitation model gives rise to the following testable hypotheses (Bar, 2003): 1) OFC, a key region where predictions are thought to be generated, should be activated early in the recognition process, before recognition is completed; 2) The gist information used to trigger the top-down facilitation process should be delivered to OFC by fast magnocellular pathways; 3) This information should compatible with magnocellular processing (e.g., contain LSFs); 4) Activity in the OFC should be predictive of recognition success; and 5) This OFC activity should be modulated by how well the global shape of a stimulus can constrain the number of alternative interpretations of the input image. In the following section we describe the studies we performed to test these hypotheses.

2.3 Activity in OFC is initiated early

The initial fMRI study examining the BOLD signal between recognized and unrecognized objects showed activation differences not only in the object recognition areas in IT, but also in OFC (Bar et al., 2001). In this paradigm, stimuli were presented very briefly, and forward- and backward-masked to make them difficult to recognize. The paradigm was structured so that after multiple repeated exposures, the stimuli that initially could not be recognized became recognizable (Bar et al., 2001). This activation of OFC for recognized vs. the same, initially unrecognized stimuli led to the hypothesis that OFC might be responsible for generating predictions about the possible identity of an object (Bar, 2003). Clearly, to facilitate the bottom-up recognition processes, top-down predictions from OFC would have to be available before the bottom-up recognition in IT is completed. Thus, activity in OFC should precede recognition-related activity in IT.

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A recent study tested this hypothesis using magnetoencephalography (MEG), a method with superior temporal resolution, with the same paradigm as in Bar et al. (2001). The results demonstrated that differential OFC activity indicative of successful recognition indeed precedes the activity in IT by 50 − 85 ms (Figure 2). In other words, OFC activity was diagnostic of successful recognition earlier than activity in the object recognition regions, supporting the critical prediction of the model (Bar, 2003). Activity peaked in the left posterior orbital gyrus at 130 ms from stimulus onset, and was statistically significant from 115−145 ms (Bar et al., 2006a).

To clarify the cortical chain of events that lead to object recognition, the synchrony between the activity in the early visual cortex and OFC, and between OFC and IT was examined. Specifically, phase-locking analysis (Lachaux *et al.*, 1999; Lin *et al.*, 2004) was used to determine whether the regions demonstrated frequency- and time-locked MEG activity. The results revealed strong phase-locking between the early visual regions and OFC at a relatively early stage, and between OFC and IT at a relatively later stage. This temporal synchrony pattern is consistent with the involvement of OFC in top-down facilitation of object recognition. Critically, the OFC-IT phase-locking was stronger and of longer duration for recognized vs. unrecognized stimuli (Figure 3). Moreover, the timing of the increased OFC-IT phase-locking coincided with increased differential activity in IT for these trials (Bar et al., 2006a). High phase-locking indicates that the trial-by-trial phase difference varies little, meaning that the phases of signals from the two areas are highly predictive of one another. This suggests that the two areas being examined are interacting, as it is unlikely that the signals would be strongly coupled if they were evoked by independent generators.

Studies examining the processing of emotional stimuli likewise have demonstrated that OFC is activated early in response to fear stimuli (Carretie *et al.*, 2006), even when subjects were not conscious of these emotional stimuli (Carretie *et al.*, 2005). These results suggest that the same processes involved in top-down facilitation of object recognition may also be involved in rapid threat detection as part of an “early warning” system. The link between the role of the OFC in top-down facilitation of object recognition and rapid threat detection will be discussed in detail in section 4.

2.4 OFC responds preferentially to LSFs

A well-established phenomenon in visual psychophysics, in which global information in an image is processed before the fine details and predominates perception under naturalistic viewing conditions, is called *global precedence* (Fink *et al.*, 1996; Fink *et al.*, 2000; Hughes *et al.*, 1996; Navon, 1977; Sanocki, 1993; Schyns & Oliva, 1994). Our previous findings showed that object recognition is associated with early activation of OFC, which suggests that its connections with the early visual regions must have relatively fast conduction velocities and thus are likely to be magnocellular. Therefore, we hypothesized that the information initially projected to OFC contains mainly global information, i.e. LSFs. Recent fMRI and MEG experiments tested this proposal by comparing activity during visual recognition of images that were low-pass-filtered to include only LSFs, high-pass-filtered to include only high spatial frequencies (HSF), or were unfiltered and included all spatial frequencies. Differential BOLD activation was found in OFC for images containing LSFs (unfiltered and LSF images), when compared with HSF images. A follow-up study using MEG revealed that this differential activity in OFC peaked between 110−140 ms after stimulus onset, corresponding to the recognition-related peak in OFC in the previously described MEG experiment that compared recognized vs. non-recognized objects (Bar et al., 2006a). It is particularly relevant that this OFC activity was highly similar for the LSF and Intact conditions, and significantly different from that elicited by the HSF images.

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Recognition in both the LSF and HSF conditions was significantly slower than for the intact images (by ~90 ms), which underscores the importance of both types of information for optimal recognition. The global-shape information carried in LSFs may trigger initial predictions in OFC; however, the fine-details provided by HSFs are typically required for converging onto a single identity of a particular object in IT. While neither the LSF nor the HSF stimuli were recognized as quickly as the intact images, the similarity between the response to intact and LSF images in OFC suggests that the engagement of OFC in top-down facilitation of recognition is dependent on the availability of LSF information, whether or not HSF information is present in the image. To test this hypothesis more thoroughly, phase-locking analysis was again used to explore the cortical interactions involved in processing the LSF-only, HSF-only, and intact images during object recognition. Strong phase-locking was found between OFC and IT at 130 ms for LSF and intact images, but no significant phase-locking was apparent between these regions for the HSF images (Figure 4). This lack of interaction between OFC and IT for images containing only HSFs again indicates that early triggering of top-down predictions from the OFC requires the presence of LSFs (Bar et al., 2006a). Similar results have been obtained in a recent electroencephelopgraphy (EEG) study, which found an interaction between spatial frequency content and emotional content for non-face stimuli in OFC at 135 ms after stimulus onset (Carretie *et al.*, 2007). Combined with the MEG results described above, these findings suggest that the activation seen in the OFC from around 100 −150 ms may be a result of a shared circuit involved in top-down facilitation of object recognition and rapid emotional processing. We discuss this possibility in greater detail in Section 4.

Understanding the patterns of information flow in the brain is critical for clarifying the mechanism underlying a particular neural process. Causality analyses (Ghuman et al., 2006; Granger, 1969) of MEG data (Ghuman *et al.*, In prep-b) can be used to infer the direction of information flow between two cortical regions by examining whether signal from one region can be predicted from past values of signal from another region. Granger causality is a well-established method in econometrics that uses an autoregressive function to determine whether the first signal can predict a second signal (Granger, 1969). Additionally, the recently developed method of directional phase-locking determines whether past phases of one signal can predict a second signal by determining the trial-by-trial variance in the phase relationship between these signals. To determine the direction of information flow between OFC and IT, both Granger causality (1969) and directional phase-locking (Ghuman et al., 2006) were used with MEG data from the studies describe above (Bar et al., 2006a). These analyses showed that there is a reciprocal exchange of information between OFC and IT, again only when LSFs are present in the image. Therefore, the bidirectional interaction between the OFC and IT probably reflects continual refinement of top-down and bottom-up information, rather than a unidirectional projection from OFC. The early top-down projection of information from OFC may focus the bottom-up processing on the likely object candidates, and the bottom-up projection from IT to OFC may be used to refine the prediction or to the representation of the image (Ghuman et al., In prep-b).

2.5 Magnocellular projections trigger top-down facilitation

In a recent study (Kveraga *et al.*, Submitted), the hypothesis that the projection from the early visual areas to the OFC relies on magnocellular pathways, either via subcortical projections or via the dorsal visual pathway, was tested explicitly by using a direct M vs. P manipulation. The paradigm used in this study exploited the fact that the M cells have high luminance contrast gain (therefore can resolve low-luminance stimuli), but are blind to color, whereas the P cells detect chromatic borders, but require higher luminance contrast (>8%; Tootell et al., 1988) to be activated by achromatic stimuli. Line drawings of objects were used to create stimuli that were either M-biased (achromatic, low luminance contrast) or P-biased (isoluminant, high

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chromatic contrast), with the proper stimulus values for the M and P conditions determined individually. Similar (M vs. P) paradigms have been used to demonstrate the role of the M pathway in directing spatial attention (Steinman *et al.*, 1997; Steinman *et al.*, 1998) and visual search (Cheng *et al.*, 2004), as well as to detect the M-pathway impairments in schizophrenia (Butler *et al.*, 2007; Schechter *et al.*, 2005).

Although the participants reported the P-biased stimuli to be more visible than the luminance-defined stimuli (because of the high chromatic contrast and higher mean brightness of the former), it took participants much longer to recognize the chromatic (P-biased) images than the low-luminance-contrast drawings. The M-biased stimuli activated OFC significantly more, while the P-biased stimuli activated the inferotemporal object recognition regions to a greater extent. The results showed that for the M-biased, but not for the P-biased, stimuli, larger BOLD signal in OFC was correlated with a reduction in recognition RT. Conversely, larger BOLD signal in IT was associated with an increase in recognition RT for the P-biased stimuli. These findings provide further support for a key prediction of the top-down facilitation model (Bar, 2003): namely, that fast magnocellular pathways connecting the early visual regions with OFC are critical for triggering top-down facilitation of object recognition. When this projection is employed, as was the case for the M-biased stimuli, recognition speed and accuracy improves along with positive signal changes in OFC. When its use is impaired, as was the case with the P-biased stimuli, OFC is unable to trigger top-down facilitation early, resulting in greater engagement of the bottom-up object recognition regions in IT and an overall slower recognition performance (Kveraga et al., Submitted).

2.6 Orbitofrontal activity correlates with predictive power of LSF stimuli

Another hypothesis stemming from the top-down facilitation model (Bar, 2003) is that the activation in OFC ought to reflect the predictive value of the input image. In other words, if the gist (LSF) image of an object has many, rather than few, possible interpretations, is this reflected in OFC activity? To test this hypothesis, the experiment was designed to compare cortical activations evoked by LSF stimuli with varying degrees of ambiguity (Schmid & Bar, In prep). The level of ambiguity was determined in a pilot study using only LSF images, in which subjects had to name 500 low-pass filtered everyday objects. The degree of ambiguity in these LSF stimuli was determined from the subjects' consistency in naming those stimuli and categorized into three levels, ranging from unambiguous (e.g., a giraffe) to highly ambiguous (e.g., a ball). A new group of subjects viewing the intact (i.e., unfiltered) version of each object in the subsequent fMRI experiment, showed greater OFC activity with higher levels of object ambiguity. This OFC activity was correlated with the behaviorally determined ambiguity level of the visual stimuli, suggesting that it is indeed associated with the number of possible interpretations of an input image (Schmid & Bar, In prep). These results demonstrate that OFC activity is modulated by how specifically an object can be identified based on its LSF representation and further supports the hypothesis that predictions generated in OFC are based on LSF information in an image (Bar, 2003).

2.7 Summary of supporting studies for the top-down facilitation model

In sections 2.3–2.6 we described the studies conducted to test the specific hypotheses of the top-down facilitation model (Bar, 2003). The first prediction, that OFC should be activated early in the recognition process, was supported by two MEG studies in which activity for successfully recognized and LSF stimuli activated OFC ~50 ms before the object recognition regions in IT (Bar et al., 2006a). Moreover, in both studies the activity in OFC showed significantly greater synchrony for successfully recognized and LSF-containing stimuli than for unrecognized or HSF-only stimuli (Bar et al., 2006a), indicating enhanced communication between the two regions for these types of stimuli. The hypothesis that the information used to trigger the top-down facilitation process should employ fast magnocellular projections was

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supported in an fMRI study by Kveraga, Boshyan and Bar (Submitted), which showed that M-biased stimuli activate OFC more than the P-biased stimuli, and that this OFC activity predicts the behavioral advantage for the M-biased stimuli. Another prediction of the model (Bar, 2003), that OFC activity is modulated by the interpretability of “gist” stimuli, was supported by an fMRI study by Schmidt and Bar (In prep), which showed that greater ambiguity of LSF stimuli evoked greater activation in OFC.

3. Links to priming, synchrony, and contextual facilitation

3.1 Top-down facilitation of object recognition is modulated by experience

The studies described above demonstrate that top-down facilitation is a critical part of object recognition (Bar et al., 2006a; Bar et al., 2001). This facilitation typically depends on accumulated experience with the visual world, as the perceiver has to have learned that a particular blurred shape could be attributed to, for example, a desk lamp or an umbrella (Figure 1). It is possible, of course, that for certain classes of natural stimuli, mostly those signifying threat (e.g., spiders or snakes), humans may have evolved innate responses. We will discuss this possibility in Section 4. However, recognition of most other visual stimuli is clearly affected by short- and long-term experience with the stimulus. Part of this experience concerns the duration for which we are exposed to a particular object, which modulates the development of expectations regarding this object. To address the question of how short-term visual experience with an object influences the nature and content of its cortical representation, we performed a study in which the duration of initial exposure to visual objects was varied and fMRI signal and behavioral performance was measured during a subsequent repeated presentation of these objects (Zago et al., 2005). The key finding in this study was a novel rise-and-fall pattern relating exposure duration and the corresponding magnitude of fMRI cortical signal. Compared with novel objects, repeated objects elicited maximal cortical response reduction when initially presented for 250 ms. However, being initially exposed to an object for a longer duration significantly reduced the magnitude of this effect. This rise-and-fall pattern was also evident for the corresponding behavioral priming. This pattern of results suggests that the earlier interval of an exposure to a visual stimulus results in a fine-tuning of the cortical response, while additional exposure promotes selection of a subset of key features for continued representation. We propose that the fine-tuning process is guided by the arrival of gradually increasing details about the visual stimulus, and is therefore an inherently bottom-up process completed in the occipito-temporal regions relatively early. The selection process, on the other hand, depends on high-level information and semantic knowledge, and is therefore guided by top-down signals originating in OFC.

3.2 Priming enhances cortical communication

With a few physiologically plausible assumptions regarding neural plasticity, the top-down/bottom-up matching processes described above can be adapted to explain how the visual system learns the causes of a particular sensory input. The top-down/bottom-up matching framework proposes that the identity of a sensory input is resolved through an iterative process where higher-level predictions as to the nature of the input are matched with lower-level representations of the stimulus. The higher-level representation is then refined based on any residual error between the higher- and lower-level representation, the updated higher-level representation is matched with lower-level representations, and this process continues until the cause of the input has been resolved. This process itself may be considered a learning process whereby an optimal representation of an input is “learned” through a trial-and-error, iterative refinement, process that takes place via top-down/bottom-up integration (Friston, 2005; Grossberg, 1999). To implement these refined representations, a mechanism for neural plasticity is required. The role of synchrony in top-down/bottom-up integration suggests an intriguing possibility of how this iterative processing may result in permanent changes in neural

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connections. Specifically, this framework proposes that increased cross-cortical synchrony reflects a better match between higher- and lower-level representations and asynchronous activity in part represents any residual error between these higher and lower level representations. If the physiological assumptions of modified Hebbian plasticity are assumed (Ackley *et al.*, 1985; Hebb, 1949), synchronous activity should lead to strengthened connectivity between regions and asynchronous activity should lead to weakened connectivity. This can be described as strengthening the processes that lead to successful matches between higher- and lower-level regions, as reflected in increased synchrony, and weakening the processes that lead to greater error in the match between higher- and lower-level regions, as reflected in asynchronous activity. This hypothesis is compatible with a “tuning” framework of repetition (Desimone, 1996; Grill-Spector et al., 2006; Wiggs & Martin, 1998), which suggests that non-critical stimulus features fall away with repetition. The asynchronous activity that falls away represents the features that are not present in the refined representation that results form the iterative top-down/bottom-up process. The features represented by the asynchronous activity may be analogous to the non-critical stimulus features in the “tuning” framework. With learning and repetition, the refined representation that results from the iterative top-down/bottom-up integration process becomes permanent. By making the refined representation permanent, when processing a learned stimulus again, the match between the higher and lower level representations will be greater and occur earlier. Therefore, with repetition the residual error in the match between higher and lower level representations should decrease. According to this framework, learning can be considered to occur not strictly at the local neural level, but rather in both the higher- and lower-level regions through refining the representations of a stimulus that emerges through the iterative top-down/bottom-up integration process.

Recent experimental results support important predictions derived from this extension of top-down/bottom-up matching to describe learning. In particular, if the mismatch between higher- and lower-level regions decreases with learning, as this framework predicts, the magnitude of neural activity should also decrease with learning reflecting decreased error signal (Friston, 2005; Grossberg, 1999). Numerous priming results have demonstrated that, as experience with a particular stimulus increases, neural activity decreases in both lower-level, visual processing regions of the temporal cortex, and higher-level regions of the prefrontal cortex involved in selection and control (Buckner et al., 1998; Dale, 2000; Desimone, 1996; Grill-Spector et al., 2006; Zago et al., 2005). Additionally, mismatch negativity demonstrates a similar reduction in activity for repeated stimuli in the auditory domain (Baldeweg *et al.*, 2004; Jaaskelainen *et al.*, 2004; Naatanen *et al.*, 2004).

A second prediction is that because learning occurs by refining the representation of a stimulus through top-down/bottom-up interactions, disrupting higher-level processes should disrupt the neural manifestations of learning at lower-levels as well. A pair of recent studies demonstrate that if higher-level processing in the prefrontal cortex is disrupted using transcranial magnetic stimulation (Wig *et al.*, 2005) or by shifting the decision rules in an object classification task (Dobbins *et al.*, 2004) the behavioral and neural manifestations of repetition learning are negatively affected both in the prefrontal cortex and in lower-level regions in the temporal cortex. Virtually all models of learning predict the disruption of learning in the opposite direction: lower- to higher-level processing. However, only the models that posit learning as refinement through top-down/bottom-up matching predict that disrupting higher-level processing will also disrupt learning at the lower levels of the processing hierarchy.

An additional prediction from this framework is that though neural activity decreases with learning, reflecting the reduced error signal, the synchrony between top-down and bottom-up regions should increase, reflecting the improved match between higher- and lower-level representations. A recent repetition priming study using MEG demonstrated that indeed,

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though neural activity in the prefrontal and temporal cortex decreased with repetition, synchrony between these regions increased from 190–270 ms from stimulus onset, peaking at 215 ms (Ghuman et al., In prep-a). Furthermore, these results demonstrated that the earlier that this synchronization between the PFC and temporal regions happens, the greater the learning-related benefit to task performance across subjects. This result supports another prediction of the top-down/bottom-up matching mechanism: that not only should learning increase the match between higher and lower level representations, but that the more learning has taken place, the earlier this match occurs.

3.3 Top-down Facilitation by Contextual Information

Objects in our environment usually are not distributed randomly, but tend to co-occur in particular situations. For example, computer mice are usually found near computers, whereas real mice are more likely to be encountered near mousetraps. Conversely, it would be unusual to find a computer mouse near a mousetrap. Recognition efficiency can be improved by using this learned information regarding the spatial, temporal, and semantic relationships between stimuli in our environment. Indeed, studies have shown that object recognition is facilitated when objects appear in their proper context (Bar & Ullman, 1996; Biederman, 1972, 1981; Biederman *et al.*, 1982; Davenport & Potter, 2004; Palmer, 1975). Knowing that you are entering a barber shop can rapidly sensitize the representations of objects that typically are found in barbershops, such as a razors, combs, and scissors, facilitating their recognition. In fact, context can modulate recognition of a target stimulus even when contextual information is presented simultaneously with the target. Several studies have demonstrated that scene identification can occur very rapidly based on the “gist” of the scene (Biederman *et al.*, 1974; Oliva & Torralba, 2001; Sanocki, 1993; Schyns & Oliva, 1994). These results suggest that contextual information may be extracted rapidly, perhaps based on coarse, global information, which would then be available to facilitate object recognition. Indeed, experimental results have shown that individual objects in a scene are easier to identify when they are visually and semantically consistent with their context (Biederman et al., 1982; Davenport & Potter, 2004; Palmer, 1975). For example, Biederman et al. (1982) demonstrated that objects were more difficult to recognize when they violated appropriate contextual relations in a given scene, such as being located in an invalid position, or being of an inappropriate size for that scene. In another experiment, Palmer (1975) showed that accuracy of naming objects increased when they were associated with an appropriate context, rather than an inappropriate one. The ability of contextual information to improve or decrease recognition speed suggests that rapidly extracted contextual information, perhaps from the gist of a scene, interacts with object information to modulate the object recognition process.

These results demonstrate that we use contextual information to facilitate recognition of objects, but how is this information represented in the brain? In a series of fMRI experiments, Bar and Aminoff (2003) compared neural activity for objects that are strongly associated with a context (for example, a bowling ball which is strongly associated with bowling alleys) to the neural activity for objects with weak contextual associations (for example, a pen, which may be found in many contexts and therefore is only weakly associated with any one context). Results from these experiments demonstrated that objects with strong contextual associations elicited greater activation than those with weak contextual associations in specific cortical regions: the parahippocampal cortex (PHC) the retrosplenial complex (RSC), and under certain task demands also the medial prefrontal cortex (mPFC). These results were consistent in all the experiments and were replicated in a recent study (Aminoff *et al.*, In press), strongly supporting the idea that PHC, RSC and mPFC form a “context network.”

While demonstrating the importance of the PHC and RSC in contextual processing, these studies left unanswered the question of how exactly PHC and RSC interact with the object

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recognition regions in the occipitotemporal cortex and mPFC/OFC to enable contextual facilitation of object recognition. This question was explored in an event-related contextual priming study in which subjects' response times and fMRI signal were measured during the recognition of individual objects that were strongly associated with a particular context (Fenske et al, 2006). Each object either represented the first instance of a particular context, or had been preceded by another object from the same (repeated) context. Facilitation of object recognition by previously seen contextually related objects was reflected by faster response times and changes in the BOLD signal for repeated-context, relative to novel-context, objects. Importantly, the BOLD signal in the OFC regions activated in prior studies of top-down facilitation of object recognition was correlated with behavioral facilitation of recognition judgments, such that the extent of priming by prior contextually related objects was associated with OFC activity. Furthermore, the activity observed in recognition-related temporal cortex regions and contextual processing regions of PHC was highly correlated with behavioral facilitation of object recognition (Fenske et al, 2006). These results support our hypothesis that contextual activation facilitates the recognition of other objects that are likely to co-appear with a target object.

These results led us to consider that objects most often do not appear in isolation; rather, we typically see them as part of scenes. These scenes usually represent a unique context that is associated with a specific set of typical objects. For example, a kitchen context would be associated with a refrigerator, a stove, a toaster, a blender, and so on. To the extent that context-based expectations may benefit the recognition of objects associated with the same setting, we extended our model of top-down influences during object recognition and proposed a mechanism for a rapid top-down influence of contextual information on object recognition (Bar, 2004). According to this mechanism, a blurred, LSF representation of the input is projected rapidly from the early visual regions and/or subcortical structures to OFC and PHC. In PHC, such image activates an experience-based guess about the present context (e.g., ‘street’, ‘conference room’). This information is then projected to IT, where it triggers the activation of the set of object representations associated with the specific context. In parallel, the same blurred image activates information in OFC that subsequently sensitizes the most likely candidate interpretations of the target object in IT (Fig 5). The intersection, in IT, between the representations of the objects associated with the particular context and the candidate interpretations of the target object typically results in a reliable selection of a single object identity. This representation is then filled with detail with the gradual arrival of high spatial frequencies.

4. Links to emotion and action preparation

4.1 Cooperation of OFC and the amygdala in processing of emotional stimuli

Stimuli with emotional cues tend to signify biologically important events, which require rapid evaluation and response. For this reason it is perhaps unsurprising that emotional stimuli are processed differently from neutral stimuli (Adolphs *et al.*, 2005; Carretie et al., 2006; de Gelder *et al.*, 2003; LeDoux, 2000; Morris *et al.*, 1999; Morris *et al.*, 2001; Morris *et al.*, 1998; Nomura *et al.*, 2004; Pourtois *et al.*, 2006; Vuilleumier *et al.*, 2003; Winston *et al.*, 2003). Emotional stimuli tend to have “priority processing”, evoking earlier and stronger responses both in the limbic areas, such as the amygdala and OFC, in the traditional visual recognition regions (Vuilleumier & Pourtois, 2007), as well as in subcortical structures associated with gating attention and eye movements, such as the pulvinar and the superior colliculus (Liddell *et al.*, 2005; Morris et al., 1998; Whalen *et al.*, 1998). This prioritization of emotional stimuli is seen even when stimuli are presented subconsciously (e.g., masked) (Morris et al., 1998; Whalen et al., 1998), in unattended locations (Vuilleumier *et al.*, 2001), or to patients who are occipitally blind (Morris et al., 2001), have parietal neglect (Vuilleumier *et al.*, 2002), or prosopagnosia (de Gelder et al., 2003). In the studies in which stimuli were filtered into different spatial

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frequency bands (Carretie et al., 2007; Vuilleumier et al., 2003; Whalen *et al.*, 2004; Winston et al., 2003), emotional, particularly threat, cues, were processed preferentially only when the stimuli included LSFs.

Recently, Bar and Neta (2006a) explored whether object stimuli can evoke danger perception based purely on low-level properties, specifically, their spatial frequency characteristics. Subjects were presented with matched, unfiltered object pictures, which were divided into two groups based on how sharp or smooth their contours were (e.g., an angular wristwatch vs. a round wristwatch). The sharp objects overall had more spectral power in HSF and less power in LSF, compared with the smooth objects (unpublished analysis). The objects were presented one by one, and subjects had to report how much they liked the objects. The sharp objects, despite being semantically identical to their smooth counterparts, were liked significantly less than the smooth objects (Bar & Neta, 2006a), and also evoked greater amygdala activity (Bar & Neta, 2007). These findings suggest that even very similar objects can be perceived as more threatening than their semantically and functionally matched counterparts, based simply on the low-level, spatial frequency, characteristics (e.g., sharp edges) of the stimuli.

These findings indicate the existence of a network that is activated by coarse information with emotional significance and may include pathways parallel to the primary visual projection, perhaps overlapping with the auxiliary vision network employed in “blindsight” patients (Cowey & Stoerig, 1995; Weiskrantz, 1996). An important role in this network is played by the amygdala, which is involved in evaluating the emotional significance of stimuli and detecting threats in the environment (Adolphs *et al.*, 1995). The amygdala comprises a group of nuclei interconnected with the sensory, as well as the prefrontal, cortices (Barbas & De Olmos, 1990; Ghashghaei & Barbas, 2002). In particular, the amygdala has massive bidirectional connections with OFC (Amaral & Price, 1984; Barbas & De Olmos, 1990; Porrino et al., 1981), with distinct input/output zones (Ghashghaei & Barbas, 2002; Ghashghaei et al., 2007). A recent study by Ghashghaei, Hilgetag and Barbas (2007) investigating the laminar specificity of OFC connections with the amygdala showed that projections to the amygdala originate in Layer 5 of OFC, consistent with feedback, and that the densest projections from the amygdala terminate in the middle layers of OFC, consistent with feedforward input. Given the existence of the reciprocal loops, it is unsurprising that the amygdala seems to share some of its functions with OFC. For example, fearful faces activate both OFC and the amygdala (Eimer & Holmes, 2002; Vuilleumier et al., 2002), and this activation is driven by LSFs (Winston et al., 2003).

Both the amygdala and OFC also have reciprocal connections with the object and face recognition regions in the anterior temporal lobe (Ghashghaei & Barbas, 2002; Ghashghaei et al., 2007). It is not established whether OFC receives emotion-related information first through its robust bidirectional connections with the amygdala (Barbas & De Olmos, 1990) and then feeds its interpretation of the initial feedforward projection back to the amygdala (as well as to IT), or whether it initially gets this information through a projection from another cortical (e.g., IT) or subcortical structure, e.g., the pulvinar or mediodorsal nuclei of the thalamus (Weiskrantz, 1996). In addition to the direct connections, the amygdala also projects to OFC indirectly, via the magnocellular division of the mediodorsal nucleus of the thalamus (Barbas *et al.*, 1991; Porrino et al., 1981; Russchen *et al.*, 1987). The function of this indirect projection is not completely clear, though lesions of the mediodorsal nucleus have been shown to disrupt long-term memory (Isseroff *et al.*, 1982; Zola-Morgan & Squire, 1985), perhaps affecting memory with emotional coloring in particular. It is also quite likely that OFC, given its major function of integrating information from a wide array of sources (Barbas, 2000; Kringelbach & Rolls, 2004) receives several subcortical projections concurrently. There is evidence for both inhibitory and excitatory projections from OFC to the amygdala, strongly implying top-down modulation of the amygdala output by OFC (Ghashghaei & Barbas, 2002).

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4.2 Potential role of OFC and the amygdala in action preparation

Both OFC and the amygdala also have connections with autonomic effector structures, which allow both regions to effect increases in cardiac and respiration rates based on the emotional content of the stimulus (Barbas, 2000; Bechara *et al.*, 1996). Both regions also have connections to motor structures such as the basal ganglia and the superior colliculus, which may be employed in fast evaluation of input with survival implications and triggering of reflexive or learned action in response. A recent pair of studies by Thorpe and colleagues (Guyonneau *et al.*, 2006; Kirchner & Thorpe, 2006) reported ultra-fast detection of objects with saccadic eye movements. The saccadic RTs were as fast as 120 ms, with the mean of less than 240 ms (Guyonneau et al., 2006; Kirchner & Thorpe, 2006), comparable to those in a spatial pop-out task (Kveraga *et al.*, 2002). The stimuli employed in these studies included animals embedded in natural scenes, and the latencies of the reported saccades make it highly unlikely that the saccades were initiated after visual analysis in the ventral visual pathway was completed. Rather, it is likely that most responses were made without the benefit of detailed ventral stream processing, but relied heavily on coarse subcortical (the superior colliculus-pulvinar-amygdala) and/or cortical processing in OFC. Guyonneau, Kirchner and Thorpe (2006) also investigated how well the subjects could identify peripheral targets at different orientations. The saccadic RTs to all 16 of the tested orientations were surprisingly orientation-invariant. This finding additionally suggests that the M-based early action system discussed in the previous section may be largely viewpoint-invariant.

The results of the studies reviewed above lead us to propose that the network employed in top-down facilitation of object perception may be part of an older system that evolved to quickly detect environmental stimuli with emotional significance. This primarily may involve scanning the environment for threat and danger cues, but also could include the detection of other survival-related stimuli, mating- or food-related cues. Once the coarse information is extracted and rapidly processed for emotional content, its output then may be shared with “typical” visual recognition processes to facilitate the bottom-up analysis. This hypothesis certainly needs further exploration in future studies.

5. Links to schizophrenia and dyslexia

5.1 The pathways involved in top-down facilitation are affected in schizophrenia

In recent years, important links have been identified between visual processing deficits in schizophrenia and impaired magnocellular function, while parvocellular processing seems to be mostly preserved in schizophrenia patients. Studies using Diffusion Tensor Imaging (DTI) (Butler et al., 2007), and evoked response potentials (ERPs) in electroencephalography (Butler et al., 2007; Doniger *et al.*, 2002; Schechter et al., 2005) have demonstrated anatomical and functional deficits in the early visual pathway. Deficits in the M-pathway function were demonstrated by psychophysical tasks in non-medicated schizophrenia patients (Keri *et al.*, 2006) and by significantly reduced BOLD signal in the M/dorsal-stream regions in first-degree relatives of schizophrenics (Bedwell *et al.*, 2004). Butler et al. (2007) found decreased fractional anisotropy (FA), a measure of the white matter integrity related to dysmyelination of axons, in the optic radiations of schizophrenia patients compared with normal controls. While this finding does not specifically implicate the magnocellular fibers, as both magnocellular and parvocellular neurons project from the LGN to the visual cortex, dysmyelination affects magnocellular neurons to a greater extent due to their thicker myelination. Furthermore, work by the same group employing psychophysical manipulations and evoked potentials has shown that schizophrenia patients exhibit significantly reduced responses in scalp potentials (P1) associated with the M pathway (Butler et al., 2007; Schechter et al., 2005). The size of the M-related P1 potential was correlated with scores on a clinical measure (ILS-PS; Loeb, 1996) used to assess how well schizophrenia patients should be able

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to function on their own. Low-functioning patients showed a reduction in the P1 component, compared with the high-functioning patients and controls (Schechter et al., 2005). The authors have used the findings of dysfunction in the M pathway to argue that the visual processing deficits observed in schizophrenia are due to impaired bottom-up (rather than top-down) processing (Butler et al., 2007). However, it is important to note that there is no disagreement between this view and our top-down facilitation model, as well as the findings that motivated and support it. The apparent incongruity is due solely to a difference in terminology and scope. Butler et al. (2007) use the term ‘top-down’ to describe processes guided by attention, pre-cued predictions and the like. However, the model the authors proposed to account for the effects of the M pathway impairment in schizophrenia proposes the same critical role for fast, M-based predictions as the top-down facilitation model (Bar, 2003).

5.2 The M pathway abnormalities in dyslexia

Reading deficits observed in dyslexia have been associated with degraded dorsal stream activity and attentional deficits (e.g., Casco, 1993; Cornelissen *et al.*, 1998; Pammer & Wheatley, 2001; Rayner *et al.*, 1995; Steinman et al., 1998). This has led to the proposal that the M pathway dysfunction is responsible for the deficits observed in dyslexia (Vidyasagar, 1999, 2004; Vidyasagar, 2005; Vidyasagar *et al.*, 2002) although this view may be still tentative (Skoyles & Skottun, 2004). Pammer (2006), using MEG, showed that the right posterior parietal cortex, a region along the dorsal visual stream receiving M projections, is activated more with higher spatial encoding requirements. Another study compared dyslexic children, who wore yellow or neutral-density filters for three months while reading (Ray *et al.*, 2005). Yellow-light filters enhance M pathway activity by blocking out the M activity-inhibiting blue light. Indeed, the children who wore yellow-light filters gained significantly in their reading ability, compared to the control group (Ray et al., 2005), supporting the observations of lower luminance contrast sensitivity (i.e., M pathway impairment) in dyslexic children (e.g., Lovegrove, 1993). However, another group (Bednarek & Grabowska, 2002; Bednarek *et al.*, 2006) found *higher* luminance contrast sensitivity in dyslexic children, which the authors interpreted as the possible cause of increased saccade frequency in dyslexic readers (Zangwill & Blakemore, 1972). While the exact nature of M pathway impairment in dyslexia is far from being resolved, there seems to be enough evidence (see Vidyasagar, 2004) to suggest that the M pathway abnormalities may lead to disrupted top-down guidance of visuo-spatial attention in reading.

6. Discussion

The primary principle that emerges from our proposal and the reviewed findings is that the brain extracts coarse, gist information rapidly, and uses it to generate predictions that help interpret that input. The focus here has been on the specific problem of visual object recognition. However, it seems reasonable to generalize that the same principle applies in many domains and modalities. To make this generalization, we will start by introducing a more global framework and terminology.

In this framework, the brain is perceived as proactive in nature: rather than waiting to be activated by sensations, it is constantly generating predictions that help interpret the sensory environment in the most efficient manner. Building on previous work, this expanded proposal posits that rudimentary information is first extracted rapidly from a perceptual input, and then used to derive *analogies* linking the input with the most similar representations in memory (Bar, In press). The linked stored representations in turn selectively activate the associations that are relevant in the specific context (Bar *et al.*, 2007), which provides focused, testable predictions. These predictions facilitate perception and cognition by pre-sensitizing representations all the way downstream to primary cortices. In other words, this framework

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relies on three main components: associations of related representations, analogies between the input and memory, and the subsequent generation of predictions. We will elaborate on each below.

Associations provide the “glue” that binds related concepts in memory. These relations and associations are inferred from knowledge accumulated with experience of recurring co-occurrences. There are many statistical regularities in our environment (e.g., traffic lights tend to be present in street contexts), and the brain uses them to short-cut processing in similar future situations. The term *analogy* refers to the mapping of a novel input to existing representations in memory. With our accumulated experience, nothing is absolutely unfamiliar to us, in that we have encountered at least some aspects of that input in the past. For example, we can recognize a train station in a foreign city, we know how to behave in a museum even if we have not been to this specific one before, and so on. The analogical operation maps the specific input to the closest representation (or collection of constituent representations) in memory. Creating this analogical link then allows us to apply our ever-evolving memories to the novel situation. Specifically, once there is an analogy between input and memory, we can make use of all the relevant information associated with this analogy. For example, imagine you see a zebra for the first time in your life. It will seem to you almost like a horse, with which you are familiar. Therefore, you can make good guesses about other properties of this new animal: how it runs, what it likes to eat, and so on. By activating the associated information, the brain generates specific predictions that can later be tested. Of course, these associations-based predictions are only an approximation. Experience with this new animal will update your representation of a zebra and its own set of associations. In many levels, repetitive experience will make these operations of analogies, associative activation and the generation of prediction automatic and require less conscious effort.

One important question for future research is how exactly can gist information be sufficient for activating predictions that are specific enough to be helpful? Given that such analogical mapping is based on coarse information, the analogy is not expected to typically be one-to-one, in that it might suggest multiple alternatives, as the model for top-down object recognition described above implies. In conjunction with other sources of information, these multiple alternatives may be further narrowed even before the thorough analysis of the input takes place. Indeed, coarse information seems sufficient for most processes to make an informed and, somewhat surprisingly, successful initial guess. When it is insufficient, contextual information, which can also be extracted rapidly (Torralba, 2003), helps resolve many remaining ambiguities (Bar, 2004). The conjunction of low spatial frequencies and context might therefore be sufficient in most situations (Fig. 5). Details seem necessary only for specific tasks (e.g., finding your keys on a cluttered counter), and otherwise many of them are filled-in by predictions rather than by perception. The framework elaborated here can help realize the role of associations, analogies and predictions in domains far beyond this of visual recognition, a few of which we will discuss here.

One example is a phenomenon termed *representational momentum* (Freyd, 1983), whereby a sequence of static photographs that implies a certain type of motion affects subjects' performance on the target image, as a function of its difference from the previous image in the sequence. A related fMRI study (Kourtzi & Kanwisher, 2000) suggests that even static images with implied motion can activate areas MT/MST, which are believed to analyze actual motion signals. Similarly, fMRI showed that different premotor sub-regions are activated depending on the properties (e.g., speed and location) of the display that had to be attended and anticipated (Schubotz & von Cramon, 2001). These results demonstrate how predictions regarding the anticipated motion of a stimulus modify the perception of and neural activity in response to seeing that stimulus.

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Such expectations-based preparatory activation has been observed in numerous domains. For example, threat of tickling activates somatosensory cortex (Carlsson *et al.*, 2000); visual imagery, which may be a critical vehicle for the generation of predictions, activates visual cortex, and has even been shown to activate early visual cortex in a retinotopically organized manner (Slotnick *et al.*, 2005), and similarly, visual imagery of higher-level objects and faces activates the same regions that are activated with the perception of the same stimuli (Ishai *et al.*, 2002; Ishai & Sagi, 1995); and gustatory cortices can be activated by pictures of food (Simmons *et al.*, 2005). Demonstrations of contextual priming (Bar & Ullman, 1996; Biederman, 1972; Davenport & Potter, 2004; Palmer, 1975) provide a further example of the generation of visual predictions, where seeing a certain object activates the representation of other objects that are likely to appear in the same context. Finally, predictions not only facilitate perception and cognition, they ultimate play a critical role in action, which is best manifested by the sequential representation and execution of action sequences (Keele *et al.*, 2003; Lisman, 1999).

In higher cognitive levels, predictions have a critical role in language comprehension and sentence integration (DeLong *et al.*, 2005; Duffy, 1986). Furthermore, being able to predict the intentions and actions of others is beneficial (e.g., ‘theory-of-mind’) (Frith & Frith, 2006; Mitchell *et al.*, 2005), and has recently been demonstrated to support sensory processing (Neri *et al.*, 2006). Predictions also play a prominent role in how we enjoy art, and music in particular (Huron, 2006).

The generation of predictions is manifested widely also in social interactions. Here the process of analogy might be especially pronounced, as we compare current occurrences with similar previous experiences. Consider first impressions, for example. People tend to make rapid evaluations of other people, based on the information that is available first, sometimes in less than 100 ms (Bar & Neta, 2006; Willis & Todorov, 2006). We propose that this process is based on information that is extracted quickly, such as low spatial frequencies (Bar *et al.*, 2006b), whereby we use these global properties to link the new person with a familiar person in memory (e.g., “who does this person look like”), even if not explicitly. Once a link is found we automatically project information such as personality attributes to the new person based simply on this analogy. Although this analogy is an approximated set of attributes, it can still be helpful when starting an interaction with a person about whom we have no other prior information. Therefore, first-impressions, too, are learned associations that are subsequently used to derive predictions based on scant information. In other words, in the realm of object recognition low spatial frequencies help us recognize a target object and predict what else might we encounter within the same context, and in social interactions cursory information might be sufficient for generating an initial guess about what to expect in a social interaction, using the same principle of activating predictions based on associations in memory. This might be a central principle that makes our cognitive brain so efficient: we take advantage of the past by informed advanced activation of memory in the service of the future. These types of analogy-based mappings of properties have been demonstrated to manifest themselves in processes ranging from perception and memory (DiGirolamo, 1997; Song & Jiang, 2005) to stereotypic judgments and prejudice (Devine, 1989), and can be guided by perceptual and conceptual similarity, as well as by goals (Hummel & Holyoak, 2003).

Predictions are not only used for facilitating perception and behavior by pre-sensitization; they are more generally used to help us construct a coherent and stable representation of the world around us. The information that reaches our cortex is degraded in many respects (e.g., compression done by the retina, as well as noise in the input and our neural pathways). In addition, it is only rarely that we need to attend every detail in the environment, but we need to know what is located where on a gross level. In both cases, using information stored in memory, predictions can fill-in what we cannot or do not invest the energy to process in detail.

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When considering the representation of predictive information, and the specific way by which their contribution is exerted, we can expand on some of the principles we mentioned earlier in the context of visual recognition. Specifically, the concept of low spatial frequency information and its potential to conserve neural resources and generate an “initial guess” can be applied at multiple levels. For example, when we want to predict how would someone we know react to something, we would predict from previous incidents that bear some similarity to the same content. It is never identical, but it may be close enough and therefore useful in guiding our actions to produce the most advantageous outcome. The concept of “gist” and its cortical representation becomes highly challenging when one considers such high levels of abstraction. By defining and testing gist representations and processing more explicitly, future research will reveal information crucial for our understanding of how general the principle of gist extraction for predictions is throughout the cognitive brain.

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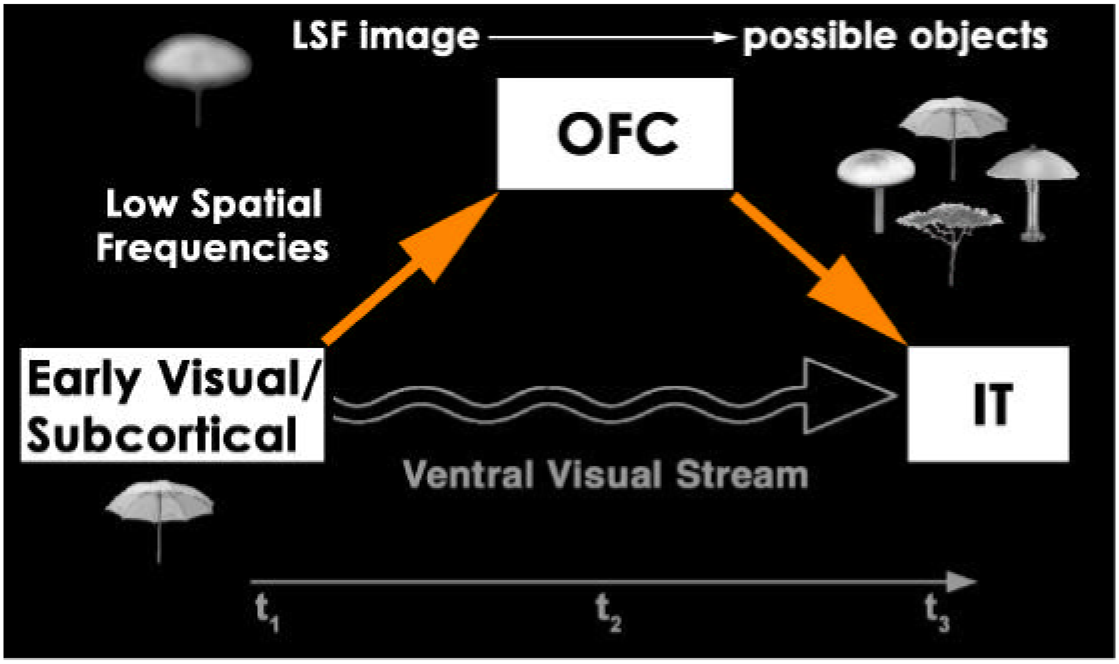

Figure 1.
Schematic of the proposed model for top-down facilitation of object recognition. According to this model, a coarse, low spatial frequency representation of the input image is rapidly extracted and projected to OFC from early visual or subcortical regions. OFC uses this low spatial frequency gist information to generate a set of predictions regarding the possible identity of the object. In parallel, detailed, systematic processing proceeds along the ventral visual stream culminating in IT. The initial guesses produced by OFC facilitate recognition by sensitizing IT to the most likely candidate objects, thereby reducing the search space that the visual system needs to consider to identify the object.

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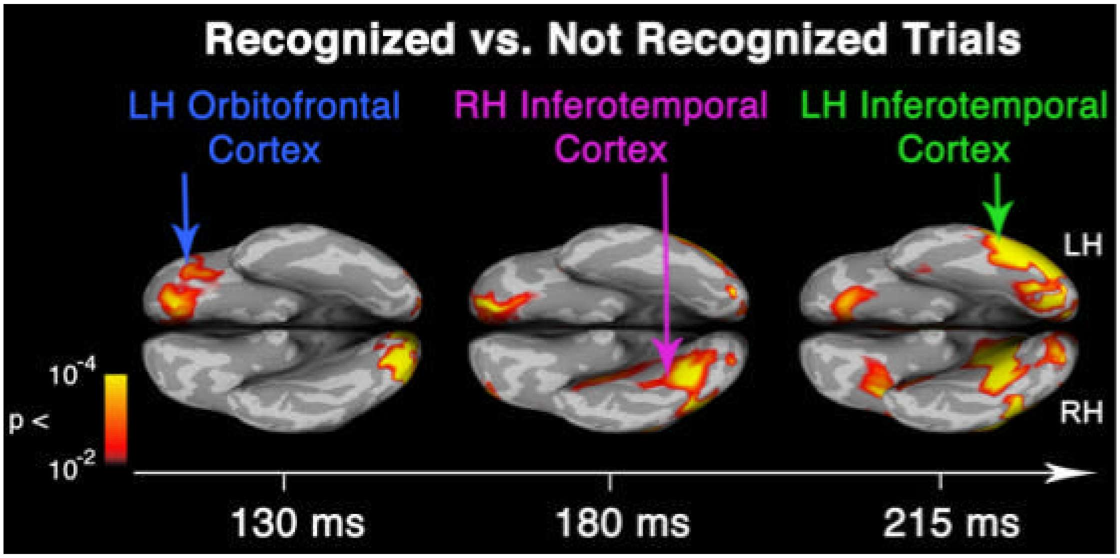

Figure 2.
MEG results demonstrate that recognition-related activity in OFC precedes IT. The left hemisphere OFC was diagnostic of recognition at 130 ms after stimulus onset, 50 ms earlier than right hemisphere IT and 85 ms earlier than left hemisphere IT. These results demonstrate that the visual response in OFC is triggered earlier than in IT, supporting the proposal that OFC generates predictions used for top-down facilitation of object recognition (Bar, 2003).

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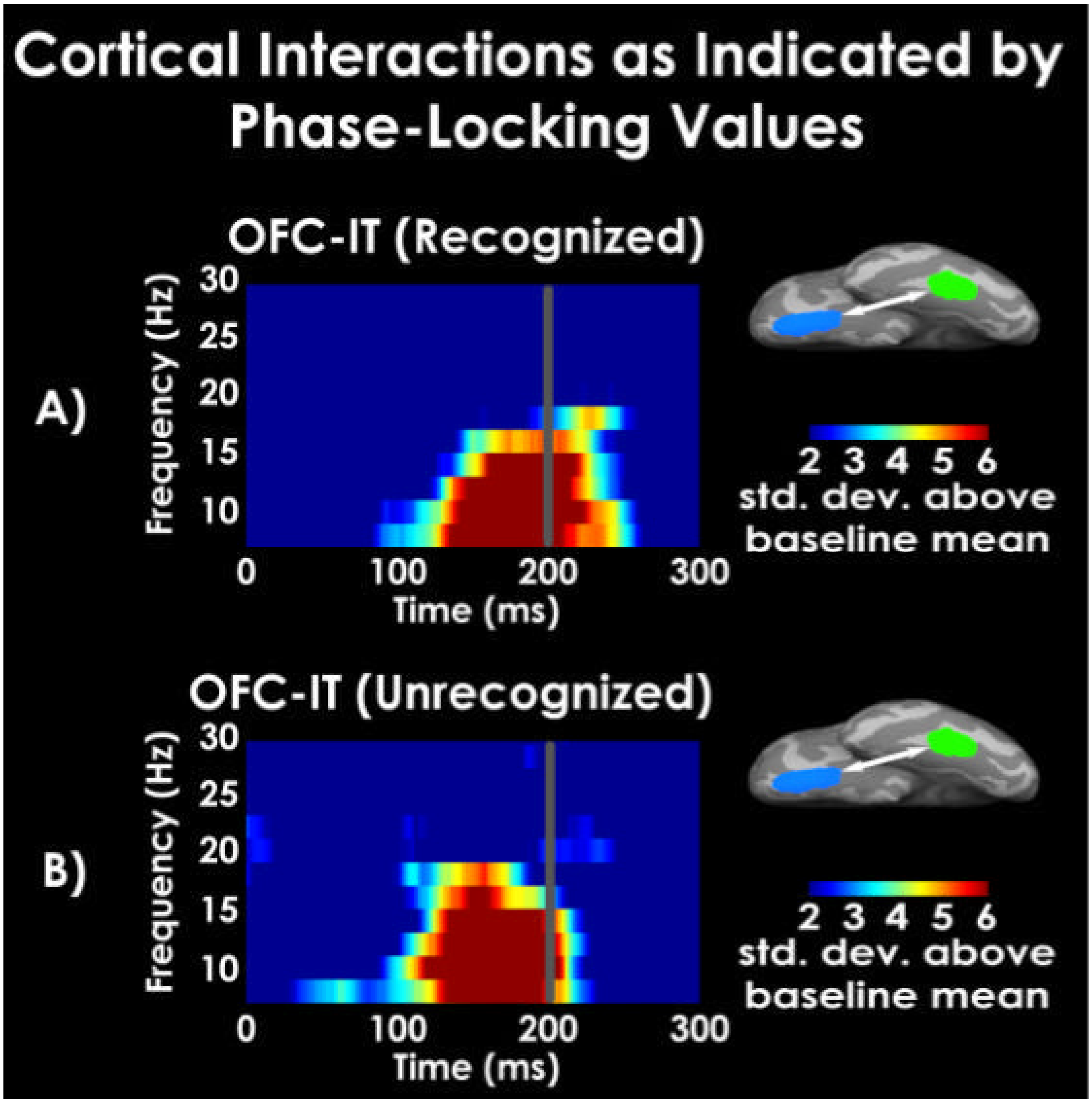

Figure 3.

Synchrony analysis demonstrating that OFC and IT form a network of interacting cortical areas involved in top-down facilitation of object recognition. A) Phase-locking demonstrates a significant interaction between OFC and IT from 130–205 ms after stimulus onset in the alpha (8.5–12 Hz) frequency band for unrecognized stimuli. B) OFC-IT phase-locking lasted 40 ms longer for recognized stimuli than for unrecognized images. C) The onset of increased phase-locking for recognized versus unrecognized stimuli approximately corresponds to the onset of recognition-related MEG activity in IT.

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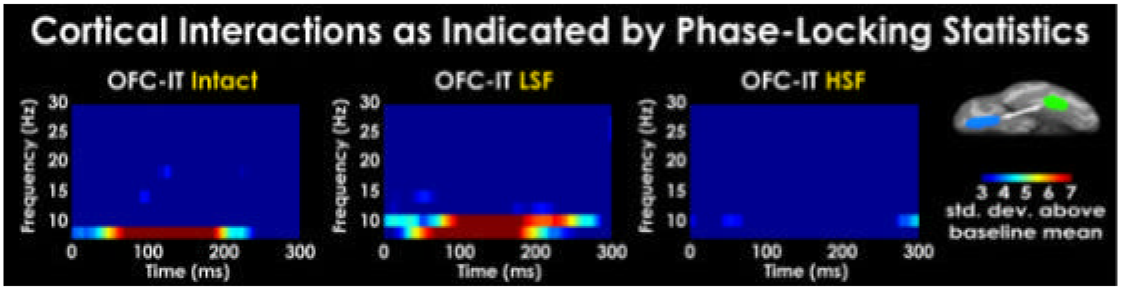

Figure 4.

Results of a phase-locking analysis comparing synchrony between the orbitofrontal and inferotemporal cortices for original, low-pass-filtered (LSF), and high-pass-filtered (HSF) pictures of objects (Bar et al. 2006). Significant cortical synchrony was found for the stimuli containing LSFs (intact and low-pass-filtered pictures), but not for HSF-only stimuli.

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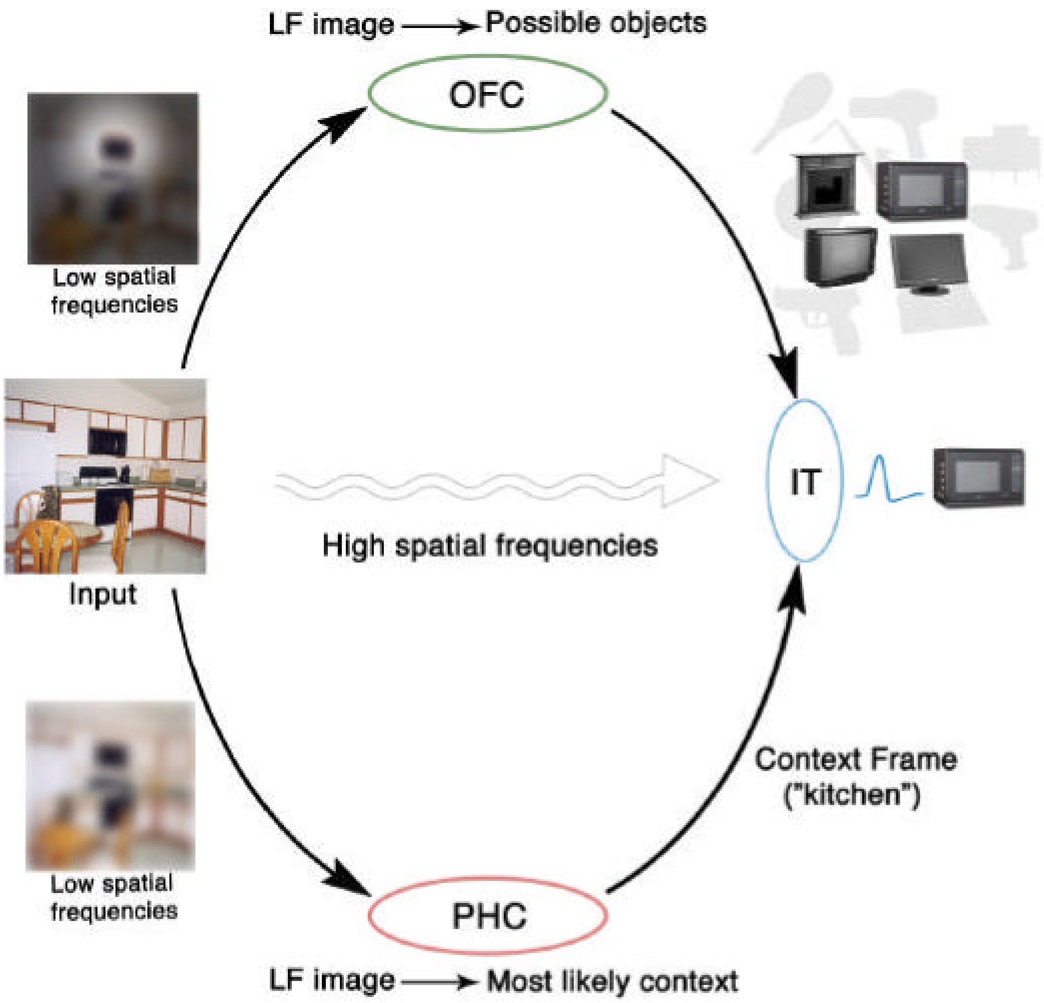

Figure 5.
Schematic of proposal of how LSF information may also trigger contextual information used in object recognition. The low spatial frequencies of the target object are projected to OFC where predictions as to the possible candidate identities are determined. In parallel, an LSF representation of the image is also projected to the parahippocampal cortex where the most likely context of the image is determined. The identity of the input image is narrowed down through the conjunction of the contextual scene, and the rapidly extracted object gist, information. Detailed information arrives later through the ventral visual stream and uses these context- and gist- based predictions to complete the recognition process.