

A Cortical Mechanism for Triggering Top-Down Facilitation in Visual Object Recognition

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Abstract

■ The majority of the research related to visual recognition has so far focused on bottom-up analysis, where the input is processed in a cascade of cortical regions that analyze increasingly complex information. Gradually more studies emphasize the role of top-down facilitation in cortical analysis, but it remains something of a mystery how such processing would be initiated. After all, top-down facilitation implies that high-level information is activated earlier than some relevant lower-level information. Building on previous studies, I propose a specific mechanism for the activation of top-down facilitation during visual object recognition. The gist of this

hypothesis is that a partially analyzed version of the input image (i.e., a blurred image) is projected rapidly from early visual areas directly to the prefrontal cortex (PFC). This coarse representation activates in the PFC expectations about the most likely interpretations of the input image, which are then back-projected as an “initial guess” to the temporal cortex to be integrated with the bottom-up analysis. The top-down process facilitates recognition by substantially limiting the number of object representations that need to be considered. Furthermore, such a rapid mechanism may provide critical information when a quick response is necessary. ■

INTRODUCTION

The ability to recognize visual objects is a crucial component of our everyday interaction with the environment. Many aspects of object recognition have been characterized behaviorally, little is known about its neural underpinnings. Here the focus is specifically on the propagation of information and analysis in the cortex during the recognition process.

Anatomical studies have shown that connections between the visual areas in the ventral pathway are ascending as well as descending. Nevertheless, the majority of the relevant research has concentrated on bottom-up analysis, where the visual input is analyzed in a cascade of cortical regions. This bias has mainly been influenced by what we know about the functional architecture of the visual cortex, which is summarized below.

The visual ventral pathway is widely believed to be responsible for shape processing for the purpose of object recognition. Neurons along this pathway differ in their feature selectivity and the size of their receptive fields. Cells in the primary visual area, V1, are organized by columns of mutual preference to basic features such as orientation and retinal location (Hubel & Wiesel, 1962). Cells in the intermediate ventral area, V4, appear to respond maximally to features of medium level of complexity such as vertices (Pasupathy & Connor, 1999), and cells in the inferior temporal cortex (IT) are more

sensitive to multipart patterns (Tanaka, 1993), viewpoint-invariant properties (Vogels, Biederman, Bar, & Lorincz, 2001), and faces (Perrett, Rolls, & Caan, 1982). This hierarchical organization results in increasingly complex processing towards the output of the ventral pathway such that cells in the anterior region of IT (TE) respond to very complex features, over large regions of the visual field.

Within the bottom-up framework, it is assumed that the visual features in the input image are first extracted in lower-level cortical areas (i.e., V1, V2, V4) and then projected to higher-level regions (i.e., IT), where a visual representation of the input image is formed (e.g., Tanaka, 1996). Presumably, recognition is achieved when the input image is associated with an object representation stored in memory. Following recognition, the object name may be also activated, depending on the task at hand, and higher-level processes such as semantic analysis and memory consolidation may take place.

In such a hierarchical model, an object is recognized only after the last visual area in the pathway for object recognition has received and analyzed all the required input from earlier areas. Therefore, this scheme emphasizes the role of the forward connections and attributes considerably less importance to the massive parallel and feedback connections that are known to exist (Rempel-Clover & Barbas, 2000; Bullier & Nowak, 1995; Nakamura, Gattass, Desimone, & Ungerleider, 1993; Porrino, Crane, & Goldman-Rakic, 1981). Recent findings, however,

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indicate that top-down mechanisms may play a central role in visual processing (Bullier, 2001; Engel, Fries, & Singer, 2001; Gilbert, Sigman, & Crist, 2001; Moore & Engel, 2001; Pascual-Leone & Walsh, 2001; Hopfinger, Buonocore, & Mangun, 2000; Miyashita & Hayashi, 2000; Siegel, Kording, & König, 2000; Rao & Ballard, 1999; Desimone, 1998; Shulman et al., 1997; Kosslyn et al., 1993).

Several previous theories have promoted the involvement of top-down analysis in cortical processing (Ullman, 1995; Kosslyn, 1994; Mumford, 1994; Grossberg, 1980). In one such top-down model (Ullman, 1995), the search for correspondence between the input pattern and the stored representations is a bi-directional process where the input activates bottom-up as well as top-down streams that simultaneously explore many alternatives. According to this model, which has largely inspired the present proposal, object recognition is accomplished when the “counter-streams” meet and a match is found.

The bottom-up flow can be seen as analogous to the extensively studied hierarchical processing; from V1 to the IT. The top-down process, however, is assumed to represent multiple possible interpretations of the input and it is less clear how such a process is initiated. Specifically, how can these high-level representations be activated before the input has been fully analyzed? Here I propose a detailed mechanism for the cortical activation of top-down processing during object recognition. In addition to providing a concrete mechanism for key aspects of previous models, the present proposal accounts for several established properties of visual object recognition and it is further used to form novel predictions.

This mechanism for the activation of top-down facilitation is comprised of three parts:

1. Low spatial frequencies (LFs) in the image are projected rapidly by anatomical “shortcuts” from early visual areas directly to the prefrontal cortex (PFC).
2. The LFs activate in the PFC simultaneous expectations about possible interpretations of the input.
3. These “initial guesses” (or multiple hypotheses; Ullman, 1995; Rumelhart, McClelland, & the PDP Research Group, 1986) are then back-projected to IT, where they activate the corresponding object representations to be integrated with the bottom-up process.

By using coarse information to provide a minimal set of possible interpretations of the input, this rapid process significantly reduces the amount of time and computation required for object recognition. In the next sections I will elaborate on this mechanism, propose a specific cortical origin for top-down facilitation, briefly mention cognitive factors that may modulate the magnitude of top-down influences in object recognition, and discuss the relationship between top-down processing and long-term visual memory.

Before delving into the details, however, it is important to note that not all models of object recognition are predicted to gain equally from a top-down process. Naturally, the benefit from a top-down rapid projection is less obvious in theories that are inherently bottom-up (Biederman, 1987; Marr, 1982). The underlying principle in these cases does not involve an exhaustive comparison of the input with multiple object representations stored in memory, but rather a direct “mapping” from visual primitives to a specific object representation. In other words, there is no explicit process of searching for a match, and therefore there is no search-space that can be reduced by a rapid “initial guess.” Nonetheless, it is conceivable that priming the correct identity in advance may be beneficial for its subsequent activation regardless of the basic components of a certain recognition model. Furthermore, early activation of an “initial guess” based only on a coarse information will certainly be helpful in extreme survival-related situations where an immediate reaction may be necessary.

A MECHANISM FOR TRIGGERING TOP-DOWN FACILITATION

Object recognition is typically accomplished within 150–200 msec from stimulus onset (not including response time). To start even earlier than that, top-down processing must use quick mechanisms and partial information (see Palmer, 1975a, for related remarks). Within the proposed framework, LFs in the image are extracted quickly and projected from early visual areas to the PFC. This projection is considerably faster than the thorough bottom-up analysis, and therefore is predicted to use especially quick anatomical connections. A possible cortical pathway to mediate this rapid projection is the *magnocellular* pathway (see also Nowak & Bullier, 1997), which is known to convey LF information (Maunsell, Nealey, & DePriest, 1990; Shapley, 1990), early (Merigan & Maunsell, 1993), and rapidly (Bullier & Nowak, 1995).

Different spatial frequencies convey different information about the appearance of a stimulus. High spatial frequencies (HFs) represent abrupt spatial changes in the image (e.g., edges), and generally correspond to configural information and fine detail. LFs, on the other hand, represent global information about the shape (e.g., general orientation and proportions). Such global information is typically sufficient for activating a relatively small set of probable candidate interpretations of the input (i.e., “initial guesses”). For example, if the only property that is extracted from the image initially is a narrow elongated blob, it will activate in high-level areas the representations that share this characteristic (e.g., a carrot, a cigar, and a pen). Figure 1 depicts examples of low-frequency images of three familiar objects. Although these pictures cannot be recognized with high confidence, there is a relatively small set of

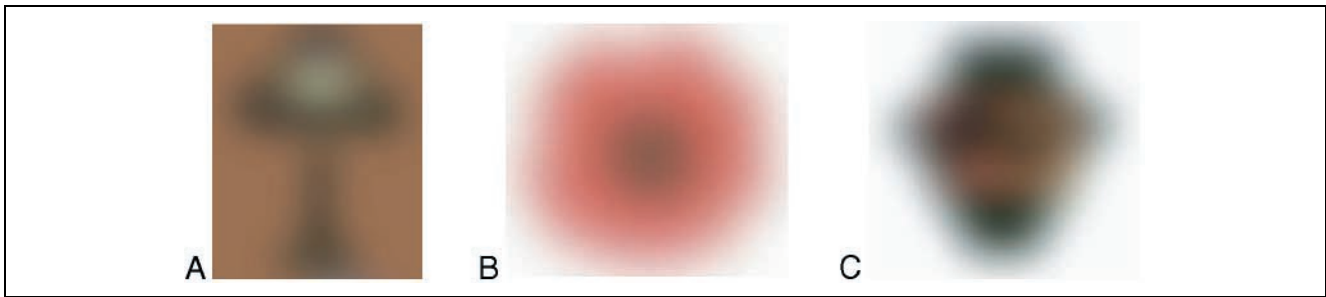


Figure 1. “Initial guesses” activated by low spatial frequency images. Three pictures of familiar and meaningful objects (256 pixels in largest dimension) were filtered to include only the LF components (0–4 cycles/picture). Although these pictures cannot be recognized with high certainty, there is only a limited set of guesses than one can produce regarding their identity. (Actual identities: A: lamp, B: flower, and C: vase.)

guesses that one can produce regarding the identity of each. For example, image 1C may be a low-frequency picture of a face, a bee, or a vase (see caption for actual identities).

Many of the representations activated by the low frequencies may be of irrelevant objects (though they all share the same global appearance with the target object). Nevertheless, such initial activation significantly reduces the number of candidate object representations that need to be considered. When the input representation is associated with one of the candidates, recognition is accomplished and the other “initial guesses” are suppressed.

Indeed, two recent neurophysiological studies (Tamura & Tanaka, 2001; Sugase, Yamane, Ueno, & Kawano, 1999) reported that activity in IT is initially broadly tuned and represents only the global features of the stimulus (i.e., the LFs). Later, 51 msec after the onset of the global response (Sugase et al., 1999), the neurons in that region also represent the fine properties of the image (i.e., the HFs). These studies provide strong support for the notion that IT initially responds to LF information before it receives HF information. In addition, results from psychophysical and physiological experiments with simple stimuli such as gratings (DeValois & DeValois, 1988; Sachs, Nachmias, & Robson, 1971), as well as with complex scenes (Schyns & Oliva, 1994), indicate that observers perceive the LF components considerably earlier than they perceive the high frequencies. A gradually increasing perception of details is also suggested by “global precedence” (i.e., the coarse-to-fine perception of information) (Hughes, Nozawa, & Kitterle, 1996; Navon, 1977), and by the pattern of reaction time observed in classification studies of objects at different levels of detail and specificity (Rosch, Mervis, Gray, Johnson, & Boyes-Braem, 1976). Finally, global and local information seem to be represented differently by the left and right hemispheres (e.g., Robertson & Ivry, 2000), and different time-courses of response between the left and the right hemispheres may give rise to the gradual coarse-to-fine perception. In summary, these data suggest that coarse information is perceived

earlier than the fine details and is therefore processed and propagated faster in the cortex.

THE CORTICAL ORIGIN OF TOP-DOWN FACILITATION

It is proposed here that the low frequencies are projected rapidly and directly from early visual areas to initiate a top-down process in the PFC. Specifically, this rapid projection of a coarse representation activates in the PFC simultaneous predictions about the identity of the input object, which are then back-projected to the temporal cortex. Several electrophysiological and lesion studies suggest the involvement of the PFC in visual recognition (e.g., Freedman, Riesenhuber, Poggio, & Miller, 2001; Parker, Wilding, & Akerman, 1998; Wilson, O’Scalaidhe, & Goldman-Rakic, 1993; Bachevalier & Mishkin, 1986), and possibly in top-down visual processing (Corbetta & Shulman, 2002; Miyashita & Hayashi, 2000; Tomita, Ohbayashi, Nakahara, Hasegawa, & Miyashita, 1999; Fuster, 1997). Here I discuss support for the specific proposal that the PFC is the most likely origin of top-down facilitation in object recognition.

Anatomical data indicate the existence of cortical and subcortical shortcuts in general. Examples include projections of coarse information from the thalamus to the amygdala (LeDoux, 1996), from V1 and V2 to V4 and the posterior part of IT (Nakamura et al., 1993), and between V4 and TE (Felleman & Van Essen, 1991). Most importantly in this context are reports showing that the PFC receives magnocellular projections (Barbas, 1995; Russchen, Amaral, & Price, 1987; Goldman-Rakic & Porrino, 1985). Specifically, the magnocellular pathway has direct connections from as early as visual area V2 to the dorsolateral PFC, and from the ventral area V4 directly to the ventrolateral PFC (Rempel-Clower & Barbas, 2000; Barbas, 1995). Therefore, these data demonstrate the existence of the neural infrastructure required for the rapid projection of LFs from the early visual cortex to the PFC.

Given our incomplete understanding of the functional subdivisions of the PFC, and the lack of data that will

allow a definition of the human homologues of the PFC regions known from the monkey, an attempt to specify the PFC modules involved in object recognition has to be considered with caution. Nevertheless, two regions seem particularly suitable for triggering top-down facilitation in object recognition: the ventrolateral PFC and the orbital PFC. They are adjacent to each other and are massively interconnected. Within the present proposal, these regions comprise a network where object-related semantic knowledge is activated in the ventrolateral PFC by the rapid projection from early visual cortex, and then transferred to the orbital PFC where expectations are generated and projected top-down.

The ventrolateral PFC has been shown to be involved in visual object analysis in monkeys (Rainer & Miller, 2000; Wilson et al., 1993). In humans, most of the existing evidence pertain to a neighboring region, the inferior frontal gyrus (IFG) within the PFC which is widely believed to be an integral part in semantic analysis of words and pictures (Miller & Cohen, 2001; Smith, 1999; Fiez, 1997; Rushworth, Nixon, Eacott, & Passingham, 1997; Buckner et al., 1995; Domb et al., 1995; Petersen, Fox, Posner, Mintun, & Raichle, 1989). Furthermore, there is an ongoing debate as to whether the exact role of the IFG is related to a competitive process between several alternatives from memory (Thompson-Schill, D'Esposito, & Kan, 1999) or to the retrieval of semantic information (Wagner, Pare-Blagoev, Clark, & Poldrack, 2001). Although this debate pertains specifically to the role of the IFG in memory processes, it is also relevant for object recognition. Additional studies may be required for the complete resolution of this debate, but note that both interpretations, competition and retrieval, are in agreement with the present hypothesis regarding the role of the PFC in top-down facilitation.

The second prefrontal candidate, the orbital PFC, is the prefrontal region that has the strongest connections with IT (Cavada, Company, Tejedor, Cruz-Rizzolo, & Reinoso-Suarez, 2000). It has been shown to be involved in analysis of visual information (Szatkowska, Grabowska, & Szymanska, 2001; Frey & Petrides, 2000; Schnider, Treyer, & Buck, 2000; Meunier, Bachevalier, & Mishkin, 1997; Voytko, 1985; Thorpe, Rolls, & Maddison, 1983). Most importantly in this context, activity in the orbital PFC has been associated with guessing, hypothesis testing, and with the generation of expectations (Petrides, Alivisatos, & Frey, 2002; Bischoff-Grethe, Proper, Mao, Daniels, & Berns, 2000; Carlsson, Petrovic, Skare, Petersson, & Ingvar, 2000; Frith & Dolan, 1997; Bechara, Tranel, Damasio, & Damasio, 1996), all of which directly support the role attributed here to this region as a potential top-down source of predictions.

The orbital PFC has been implicated also in the selection of currently relevant memories and goal-driven activity (Schnider et al., 2000), as well as in processing reward-related information (e. g., Tremblay & Schultz,

1999). Therefore, it is possible that at least some regions within the orbital PFC are sensitive not only to the actual properties of objects but also to the combination of these properties with a relevance value, derived from the integration of input signals to it from the ventrolateral PFC, the amygdala, and possibly other structures.

An early activation of knowledge related to the input image has obvious advantages for producing expectations about the environment, which can facilitate perception and action by focusing the cortical processing. This is especially pronounced in situations such as danger, where we need to analyze the image of an approaching lion, for instance, as quickly as possible, activate related semantic information that allows us to infer danger, and then immediately share this information with other areas relevant to our subsequent decision and action. Interestingly, the orbital PFC has been shown to respond selectively to images of angry faces, but not to sad or neutral faces (Blair, Morris, Frith, Perrett, & Dolan, 1999) and this activation was proportional to the magnitude of the anger expressed by the faces. Indeed, that the orbitofrontal PFC is part of an orbitofrontal–amygdala–IT triad (Ghashghaei & Barbas, in press; Morecraft, Geula, & Mesulam, 1992) and that it has massive reciprocal connections with other limbic areas, the autonomic motor system, and premotor areas (Ghashghaei & Barbas, in press; Cavada et al., 2000; Rempel-Clower & Barbas, 1998; Carmichael & Price, 1995; Amaral & Price, 1984) support the hypothesis that the early projections to the PFC are beneficial for identification of danger (see also Gray, Braver, & Raichle, 2002 for another demonstration of integration of cognition and emotion in the PFC).

Given the multimodal inputs to the orbital PFC, it is believed to represent a constantly updated global view of the environment. The early expectations projected top-down from the orbital PFC, therefore, serve multiple purposes. First, they may facilitate perception by producing narrow predictions and project them “downstream” via the rich reciprocal connections between the orbital PFC cortex and sensory areas. Second, they may facilitate avoidance and fight-or-flight response via the orbitofrontal connections with the limbic system.

It is not clear whether object-related representations in the PFC contain the same visual information as the object representations in IT, or whether these PFC representations are more abstract. On one hand, the PFC has been repeatedly shown to represent and analyze semantic and abstract information. On the other hand, accumulating reports suggest the existence of visual representations in the PFC (Szatkowska et al., 2001; Frey & Petrides, 2000; Rainer & Miller, 2000; Schnider et al., 2000; Smith, 1999; Greenlee, Koessler, Cornelissen, & Mergner, 1997; Rushworth et al., 1997; Goldman-Rakic, 1995; Wilson et al., 1993). A conceivable alternative is that the PFC translates the rapid projection of sensory information into pointer-like signals that activate the

corresponding visual representations in IT. Although one can only speculate on the exact nature of such a mechanism at the moment, this alternative seems plausible given the work of Miyashita and Hayashi (2000) and Tomita et al. (1999), demonstrating the existence of prefrontal signals that trigger memory retrieval of visual object representations in IT. Therefore, it is possible that the PFC representations of objects are not as detailed as those in IT, but are still sufficient to activate expectations based on coarse information.

Finally, a recent report demonstrating the central role of the PFC in representing categories of visual objects (Freedman et al., 2001) is in direct agreement with the present proposal that a visually driven PFC activation is elicited by LFs. The findings of this study indicate that PFC representations distinguish between objects belonging to different categories, but not between individual objects within the same category. Such exemplar-specific detailed shape information has been shown to be represented instead in IT (Op de Beeck, Wagemans, & Vogels, 2001; Tanaka, 1993). In other words, the PFC represents relatively coarse visual information that can mediate between-category decisions. Indeed, a Doberman and a Schnauzer, for example, will both be categorized as dogs even when their image is blurred (i.e., composed of LFs), and at the same time will be distinguishable from cats (Figure 2). Therefore, LF images generally contain the information required for distinguishing even between members of highly related categories.

Another aspect of the present proposal is that the projection of low-frequency information to the PFC is rapid. This is supported by the finding that category-specific activation in the PFC starts about 100 msec from stimulus onset (Freedman et al., 2001; see also Marinovic, Trebon, Chauvel, & Halgren, 2001; Rainer & Miller, 2000; Thorpe, Fize, & Marlot, 1996; Halgren et al., 1994; Funahashi, Bruce, & Goldman-Rakic, 1990; Thorpe et al., 1983). Such early category-specific activation may further reflect the neural mechanism responsible for the relatively shorter time required to name objects in their basic-level name (e.g., a dog) compared with naming objects in their sub-ordinate name (e.g., German Shepherd) or super-ordinate name (e.g., an animal) (Rosch et al., 1976).

To summarize, given that: (1) the magnocellular pathway projects LF images early and directly from the visual cortex to the ventrolateral PFC, (2) the ventrolateral PFC is associated with semantic processing and possibly with visual representations, (3) the ventrolateral PFC is massively and reciprocally connected with the orbital PFC, and (4) the orbital PFC is involved in producing guesses and expectations, and it has direct projections to area IT and to the amygdala, the network illustrated in Figure 3 may be proposed.

FACTORS THAT MODULATE TOP-DOWN EFFECTS

Although top-down facilitation is suggested to be an integral part of recognition, its role and magnitude can be modulated by task demands and prior expectations. One rationale for this proposal is the findings of an fMRI study of explicit object recognition (Bar et al., 2001). This study indicated that prefrontal activation was present in all recognition conditions, especially in the IFG and the orbital gyrus. But it was significantly more pronounced when the recognized images were presented briefly and were masked, compared with the easier recognition of nonmasked objects. This may suggest that the extent of top-down facilitation may be affected by task demands. In other words, when recognition is difficult (e.g., brief and masked presentations, low contrast, or occluded objects), the interpretations conveyed by the top-down process are based on a coarser and less accurate information, an uncertainty that will result in a broader set of “initial guesses.”

If the PFC (and top-down processing) is less involved when recognition is easy, how does it “know” not to be active? When recognition is sufficiently easy, it may be accomplished by the bottom-up analysis so quickly that top-down facilitation does not have sufficient time to develop. Alternatively, it is conceivable that when recognition is easy, considerably fewer candidates are activated, resulting in a lower level of PFC activation.

Context and prior expectations regarding the identity of objects are additional factors that may affect the magnitude and dynamics of top-down influence during recognition (Biederman, 1981; Palmer, 1975b). While it is suggested that a top-down process that is based on the



Figure 2. As long as the members of each category look similar to each other and significantly different from members of other categories, which is most often the case (Rosch et al., 1976), LFs are generally sufficient even for object categorizations (e.g., dog or cat). This supports the present proposal that LF object representations are sufficient for mediating the categorical distinctions made by PFC neurons (Freedman et al., 2001).

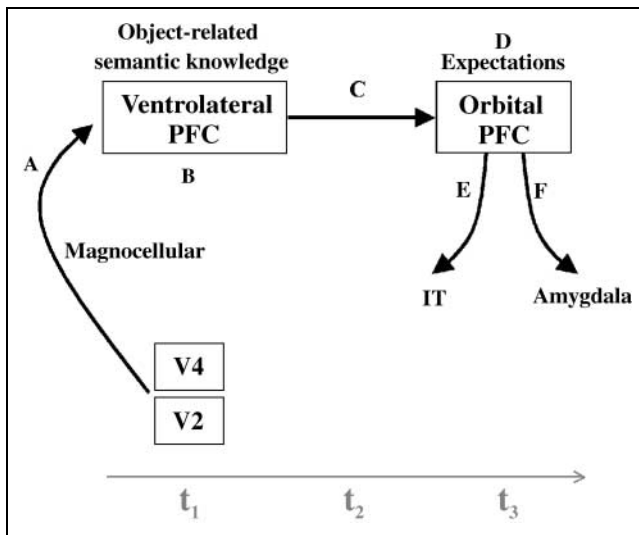


Figure 3. A schematic illustration of the proposed model. The triggering of top-down facilitation progresses in the temporal order t_1 , t_2 , t_3 . Afterwards, information transfers in all these pathways in a reciprocal manner. Support for each component of this diagram includes: (A) Rapid magnocellular projection from early visual cortex to the ventrolateral PFC (Rempel-Clover & Barbas, 2000; Goldman-Rakic & Porrino, 1985); (B) Activation of object-related semantic knowledge in the ventrolateral PFC (Freedman et al., 2001; Petersen et al., 1989; Smith, 1999; Fiez, 1997; Demb et al., 1995); (C) Direct projections from the ventrolateral to the orbital PFC (Fuster, 1997; Barbas & Pandya, 1989; Goldman-Rakic, 1987); (D) Activation of expectations in the orbital PFC (Petrides et al., 2002; Frith & Dolan, 1997); (E) Direct anatomical connections between the orbital cortex and IT (Rempel-Clover & Barbas, 2000; Morecraft et al., 1992); and (F) Direct anatomical connections between the orbital cortex and the amygdala (Ghashghaei & Barbas, in press). For the sake of simplicity, this figure shows only a subset of areas and connections, and additional but unrelated functions that are mediated by these anatomical structures are not discussed.

rapid projection of LFs facilitates recognition by reducing the number of models that need to be compared with the input, context and prior expectations may reduce this search-space even further by providing a more “educated guess.” A mechanism for producing such context-based “educated guesses,” and their use in disambiguating the LF-based “guesses” is proposed later.

TOP-DOWN FACILITATION AND VISUAL MEMORY

Seeing an object once improves its recognition in subsequent encounters, a phenomenon termed “priming” (Schacter & Buckner, 1998; Tulving & Schacter, 1990). This improvement with experience may entail the strengthening of certain cortical representations using long-term synaptic modifications (e.g., Bar et al., 2001; Wiggs & Martin, 1998). Although top-down facilitation entails the coactivation of multiple object representations, possibly in both the PFC and IT, it is further proposed here that only the selected representation is eventually primed. In other words, priming starts only after a single representation from the candidates “sug-

gested” by the top-down process has been selected. This prediction is consistent with results from studies that used ambiguous words that have multiple possible interpretations, where only the contextually relevant meaning was primed (Simpson, 1984; Seidenberg, Tanenhaus, Leiman, & Bienkowski, 1982). The following physiological findings offer further support for this idea of selective priming.

Several studies (Kovács, Vogels, & Orban, 1995; Rolls & Tovee, 1994) have demonstrated that the neural response to even a briefly presented picture lasts for 200–300 msec. Analysis using techniques from information theory (Tovee, Rolls, Treves, & Bellis, 1993) suggests that although most of the information that seems to be sufficient for recognition is already present in the first 100 msec of the neural response, the relevant activation continues for 200–300 msec. This extended interval may reflect the duration that is required for priming of the chosen alternative, which starts only after this single alternative has been selected from among the multiple candidates (see Subramaniam, Biederman, & Medigan, 2000, for a long-term memory account of the prolonged activation).

The next time we see the same object, the primed connections will facilitate recognition by promoting the propagation of a single interpretation from among the several alternatives. Indeed, the reduced activity for familiar objects, termed “repetition suppression” (Rainer & Miller, 2000; Buckner et al., 1998; Demb et al., 1995; Li, Miller, & Desimone, 1993), might indicate that fewer alternatives are activated in subsequent encounters with familiar stimuli, both in the PFC and IT. It can thus be seen as a better “initial guess” due to a memory that preserves the outcome of the top-down process from previous encounters with this image. Consequently, the neural modifications that are elicited by priming facilitate (perhaps even automatize) access to the most likely representation. In agreement with this idea is a recent neurophysiological finding that repetition suppression of PFC response to visual stimuli is directly correlated with improved performance (Rainer & Miller, 2000).

PREDICTIONS AND OPEN QUESTIONS

Several testable predictions stem from the proposal presented here:

1. Object recognition entails two peaks of activation in the PFC. One is early and related to the activation of an “initial guess,” and the second is relatively late and reflects post-recognition activation of conceptual knowledge related to the recognized object. A recent study (VanRullen & Thorpe, 2001) although focused on bottom-up processing, provides initial support for this prediction.

2. The early recognition-related activity in the PFC is determined by the LF content of the input image. Only

the post-recognition, relatively late part of the PFC response is modulated also by the HFs.

3. The top-down process is suggested to facilitate object recognition by reducing the number of possibilities that need to be considered. Therefore, an absence of the top-down process is predicted to slow object recognition (i.e., prolong reaction times), but not to preclude successful recognition. In other words, object recognition in this case will rely solely on the bottom-up process. Studies of patients with lesions in the frontal cortex (e.g., Richer & Boulet, 1999; Greenlee et al., 1997; Tartaglione, Oneto, Manzano, & Favale, 1987) support this prediction. In extreme cases (e.g., when most of the object is occluded or camouflaged), however, recognition may be rendered impossible without the top-down process.

Two important questions remain open and their resolution in the future will be critical. First, it is not clear what is the exact nature of object-related representations in the PFC. Several types of representations, with a varying degree of visual specificity, may be capable of mediating the top-down facilitation proposed here. Of specific interest is the interaction between those representations and the mechanism that generates expectations based on LF images.

A second open question is: What is the role of the magnocellular projection from early visual cortex to IT? Is that specific projection also part of top-down facilitation (Nowak & Bullier, 1997), more related to the bottom-up process, or does it mediate the integration of both processes? Given that initially similar magnocellular information is projected from the early visual cortex simultaneously both to IT and to the PFC, the following expansion may be proposed.

An ambiguous object can be identified when placed in the proper spatial relationship with a related object, sometimes even when that other object is ambiguous as well (Bar & Ullman, 1996). This implies that an LF image of an object can become identifiable more easily within the context of its surrounding objects (given that the specific configuration is sufficiently typical; Biederman, 1981). For instance, a blurred image that looks like a dark box may be interpreted either as a television or as a microwave. If this target object appears next to a horizontal rectangular blob that looks like a couch, we would infer that the target object is a television. If, on the other hand, it is seen next to a vertical rectangular blob that looks like a refrigerator, the same blurred target would be perceived as a microwave.

Such a powerful effect of context may be used to select the most likely candidate from among those that are projected top-down based on LF appearance. The magnocellular projection activates in IT the representations of all the objects that look similar when blurred (e.g., a television and a microwave). In the PFC, the same magnocellular projection will activate not only the rep-

resentations of the actual candidates (possibly in a less detailed form than in IT), but also semantic information that can invoke expectations about other objects that typically coappear in each of the contexts established by the candidate representations (e.g., a couch for “living room” and a refrigerator for “kitchen”). In other words, the selection of the proper identity during recognition may be facilitated by inferring from the presence of other blurred “blobs” which of the several candidates is most likely to be present in the specific configuration. Such a “cross-product” of information about general appearance with contextual knowledge is a promising and plausible mechanism for facilitating object recognition. In fact, although future studies are required to address this issue, it seems that in most situations a blurred image of an object and its corresponding context alone are sufficient for successful recognition.

On a final note, while it is proposed that initially multiple possible representations of the input object are coactivated, our conscious perception of an object’s identity is nevertheless abrupt. In other words, during typical object recognition in our environment, we seem to become aware of the identity only after the subserving cortical processes have reached a sufficient level of certainty and converged onto a single interpretation. Indeed, awareness of an object’s identity has been suggested to be associated with gradually increasing, rather than abruptly changing, cortical activity (Bar et al., 2001), and the time before awareness may be the time during which the most likely interpretation is selected.

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