

Semantic Processing Precedes Affect Retrieval: The Neurological Case for Cognitive Primacy in Visual Processing

Justin Storbeck
University of Virginia

Michael D. Robinson and
Mark E. McCourt
North Dakota State University

According to the affective primacy hypothesis, visual stimuli can be evaluated prior to and independent of object identification and semantic analysis (Zajonc, 1980, 2000). Our review concludes that the affective primacy hypothesis is, from the available evidence, not likely correct. Although people can react to objects that they cannot consciously identify, such affective reactions are dependent upon prior semantic analysis within the visual cortex. The authors propose that the features of objects must first be integrated, and then the objects themselves must be categorized and identified, all prior to affective analysis. Additionally, the authors offer a preliminary neurological analysis of the mere exposure and affective priming effects that is consistent with the claim that semantic analysis is needed to elicit these effects. In sum, the authors conclude that the brain must know what something is in order to know whether it is good or bad.

Even before we can identify something we may like or dislike it. (Arnold, 1960, p. 36)

In fact, it is entirely possible that the very first stage of the organism's reaction to stimuli and the very first elements in retrieval are affective. It is further possible that we can like something or be afraid of it before we know precisely what it is. (Zajonc, 1980, p. 154)

Much of sensory processing, at least through the brain systems that are concerned with object identification (whether by sight, sound, smell, taste, or touch), can be seen to have the goal of enabling the correct reward value to be decoded and represented *after* the object has been identified. (Rolls, 1999, pp. 6)

These three quotes exemplify divergent opinions in how to characterize the interaction of cognition and emotion, especially during the earliest stages of stimulus encoding. Arnold (1960) suggested that people may be capable of evaluating stimuli before such stimuli are identified. Zajonc (1980), in a seminal paper, made an even stronger case along these lines. Many

recent lines of evidence seem consistent with, if not supportive of, the affective primacy position advocated by Zajonc. For example, researchers have pointed out that evaluations are often automatic (Bargh, 1997), that people often feel strong disgust without a rational basis for such feelings (Haidt, 2001), and that people appear to be evolutionarily prepared to respond to potential threats quickly, automatically, and indeed unconsciously (Öhman, 1997). Much of this work has pointed to the highly publicized subcortical route to evaluation identified by LeDoux (1996, 2000). In sum, the citations above would seem to suggest that Zajonc was probably correct when he suggested that affect retrieval often precedes semantic categorization and identification processes.

In evaluating the relationship between affect and object identification, it is useful to outline several distinct, yet related, theoretical positions. A first important question pertains to causal precedence. To the extent that one route of processing—either affect or object identification—requires output from the other route of processing in order to make its computations, then the latter route must be causally prior to the former route. The cognitive primacy hypothesis (Lazarus, 1984) is a theoretical position of this causal type: Semantic processing must precede affective processing. If, on the other hand, there is no early interaction between these two routes

Justin Storbeck, Department of Psychology, University of Virginia; Michael D. Robinson and Mark E. McCourt, Department of Psychology, North Dakota State University.

The authors acknowledge support from NIMH (MH 50074 and MH 068241) as well as input from Gerald L. Clore and Jeanine Stafanucci.

Correspondence concerning this article can be sent to Justin Storbeck, Department of Psychology, PO Box 400400, Charlottesville, VA 22904. E-mail: storbeck@virginia.edu

of processing, then the primacy of either route cannot be causal, but it can be temporal. Specifically, given an assumed independence of affect and identification processes, it could be that one route is typically faster. If so, its achievements will tend to be temporally prior to those of the other route. The affective primacy hypothesis (Zajonc, 1980, 2000) is a theoretical position of this temporal type: Affective processing is typically faster than semantic processing.

It is striking that the two camps of scholars—that is, those favoring affective primacy and those favoring cognitive primacy have largely ignored or dismissed each other's arguments rather than conduct the necessary type of comparative empirical research to settle the debate (Leventhal & Scherer, 1987). The main purpose of this review is to bring to attention sources of data that, while rarely cited within the cognition and emotion literature, are highly relevant to questions of primacy. In contrast to the widespread notion that the affective primacy issue has been settled in favor of affective primacy (e.g., Bargh, 1997), we instead argue that available data in fact support the primacy of semantic processing and do so in both the causal and temporal senses outlined above. Our position is consistent with a number of important, albeit less celebrated, recent reviews of the literature (Clore & Ortony, 2000; Robinson, 1998; Rolls, 1999).¹

The Neural Primacy of Semantic Analysis: An Overview

Neuropsychological studies can provide insight into both the time course and brain regions involved in most mental processes. Those related to object identification and affect are no different in this respect. Therefore, it will be fruitful to consider *what* happens in the brain, as well as *when* it happens, when a person views a visual object. This review will focus on neurological evidence related to the visual processing of stimuli and does not seek to be exhaustive in all respects. From the outset, for example, we should point out that we will not be centrally concerned with the dorsal visual stream, which appears to mediate object location, but not object identification, functions (Goodale & Milner, 1992). We also note that our review, given

space limitations and available data, is relatively specific to vision (e.g., vs. audition).²

The amygdala is thought to play a very important role in processing the affective significance of stimuli (see, Aggleton, 2000, for a comprehensive review). Our goal is not to review all of the amygdala's functions. However, we will focus on this structure in relation to arguments in favor of affective primacy (Bargh, 1997; LeDoux, 1996; Zajonc, 2000). Along these lines, we will suggest that the amygdala, the celebrated seat of affective primacy, relies heavily on semantic processing performed within the visual cortex.

Visual Processing

The visual cortex does the lion's share of the work related to discriminating objects, a critical first step in determining an object's affective significance. Even LeDoux (1996), who has championed a noncortical route, views the cortical route as more important in a majority of emotional situations. For this reason, it is fruitful to examine, in some depth, how visual processing occurs within the visual cortex. In particular, we will be concerned with whether there is evidence for the temporal and functional priority of semantic or affective analysis. We will suggest that the evidence is fairly strong in suggesting that semantic achievements (e.g., object identification) occur prior to affective

¹ Observers of the debate between Lazarus (1984) and Zajonc (1984) have generally concluded that the resolution of the debate may hinge on definitional issues, specifically as related to cognition and emotion (e.g., Leventhal & Scherer, 1987). Although we agree that definitional issues are important, we also suggest that certain core aspects of the debate are as essential today as they were 20 years ago. Specifically, we are concerned with issues concerning the causal and temporal precedence of object identification and affect retrieval processes. These precedence issues continue to give rise to strong theoretical statements (e.g., LeDoux, 1996; Rolls, 1999) and continue to influence multiple areas of psychology in both profound and subtle ways.

² We will use the term "semantic" to describe the meaning analysis that we propose precedes affective analysis. What we have in mind specifically are at least three achievements: (a) the integration of multiple features of the object into a single "object" code; (b) the identification of this object; and (c) the categorization of the object (e.g., as animate or not). The term semantic, then, refers somewhat more directly to the achievements of area IT (especially invariance, identification, and categorization) that seem to occur in order for a person to retrieve affective associations.

achievements (e.g., determining that the object is bad). We will also suggest that the amygdala's ability to respond on the basis of the affective significance of an object seems to require prior analysis by the visual cortex. Finally, we will suggest that much, if not all, of the processing by the visual cortex is unconscious in nature, which in turn can account for the production of unconscious affect.

Categorization

Later stages of the visual cortex, such as the inferior temporal cortex (area IT), appear to categorize visual stimuli. Such achievements by area IT are relatively sophisticated, such that it is insufficient to characterize such achievements as mere perception. Rather, objects appear to be categorized and identified within later stages of the visual cortex. Because processing within area IT is not influenced by the valence of stimuli (e.g., Rolls, 1999), available data suggest that visual categorization occurs prior to affect retrieval. These points are substantiated next.

Categorization involves matching objects in the world to certain "global" templates. Area IT responds to such global templates. In one study, monkeys were shown various shapes as well as human and monkey faces while neurons were recorded in area IT (Sugase, Yamane, Ueno, & Kawano, 1999). One group of neurons responded selectively to both types of faces. This is akin to a global template for faces, irrespective of the species of the faces. Such neural activity peaked at 45 ms poststimulus onset (Sugase et al., 1999). Additionally, a second group of neurons responded selectively to shapes, rather than faces. Because distinct neurons responded to faces versus other shapes, the evidence suggests that categorization, at least with respect to this distinction, is occurring within area IT.

Similarly, among humans, specific neuron populations in the later stages of the visual cortex appear selective for certain classes of stimuli. Studies using imaging procedures have found that the right fusiform gyrus is sensitive to faces (and other highly practiced classes of stimuli: see Gauthier, Behrmann, & Tarr, 1999), whereas the left fusiform gyrus has been found active for nonface objects (e.g., houses, cars, etc.) (Farah, Humphreys, & Rodman, 1999;

Kanwisher, 2000; Vuilleumier, Henson, Driver, & Dolan, 2002). Furthermore, within the lateral occipital cortex (LOC), distinct loci appear to be activated by distinct classes or categories of objects (Damasio, Grabowski, Tranel, Hichwa, & Damasio, 1996; Herath, Kinomura, & Roland, 2001; Martin, Wiggs, Ungerleider, & Haxby, 1996). For example, several studies have found distinct areas of selective activation for faces, tools, animals, and/or letter strings and words (Chao, Haxby, & Martin, 1999; Damasio et al., 1996; Martin et al., 1996; Puce, Allison, Asgari, Gore, & McCarthy, 1996).³

Similarly, localized lesions within specific areas of area IT produce very specific objective recognition deficits such as prosopagnosia or the failure to recognize faces (Damasio, 1990; Duchaine & Nakayama, 2005; Moscovitch, Winocur, & Behrmann, 1997; Tranel, Damasio, & Damasio, 1997). Moreover, other evidence also exists to suggest that categorization activity within area IT occurs even with respect to non-perceptual features of objects (e.g., Lee, Graham, Simons, Hodges, Owen, & Patterson, 2002). The latter data are particularly important because they show that area IT groups objects according to nonperceptual (i.e., semantic) sources of meaning as well as more perceptual sources of similarity.

Just as neuron populations within areas of the visual cortex show specificity for different classes of objects, a similar point can be made with respect to words and letter strings. First, letters and words are processed in distinct areas from faces and visual textures; specifically, words and letter strings lead to more activation in the postlateral fusiform gyrus, left lateralized (Herbster, Mintun, Nebes, & Becker, 1997; Puce et al., 1996). Posterior areas of the fusiform gyrus appear to respond equally to words and nonwords. However, more anterior sections begin to differentiate between words and nonwords, seemingly reflecting semantic processing (Nobre, Allison, & McCarthy, 1994; Price, Wise, & Frackowiak, 1996). Areas STS and posterior MTG in the visual cortex distinguish

³ We should note that we are not suggesting that every category or class of stimuli is perfectly represented by distinct groups of neurons within the visual cortex. However, we do note that there is sufficient evidence to suggest that certain classes of stimuli (e.g., faces) are in fact represented by distinct group of neurons within the visual cortex.

between orthographical and nonorthographical stimuli (Herbster et al., 1997; Price et al., 1996). Thus, the visual processing system performs a rather sophisticated analysis of letter strings, based on grammatical and orthographic conventions. We would say such letter strings were *categorized* by the brain, a necessary precondition for identification and affect retrieval (Strange, Henson, Friston, & Dolan, 2000).

There is no reason to believe that the categorization processes performed by area IT are conscious. Indeed, on the basis of ERP data, we might conclude that unconscious categorization routinely precedes conscious categorization. Furthermore, unconscious categorization by the visual system may occur extremely quickly after stimulus exposure, in as little as 48 ms for “global templates” (Sugase et al., 1999) and 70–80 ms for classes of stimuli (Van Rullen & Thorpe, 2001). Interestingly, Van Rullen and Thorpe (2001) also found that the initial (70–80) categorization-related ERP component was not highly correlated with a participant’s response to the task at hand, whereas an ERP component that occurred at 190 ms poststimulus onset was. Thus, categorization appears to occur quite rapidly and seems to occur independently of later, possibly more conscious, categorization processes. Relatedly, people can classify objects on the basis of category membership even with no awareness of the distinct categories guiding their response (e.g., Reed, Squire, Patalano, Smith, & Jonides, 1999).

In summary, we conclude that categorization occurs within later stages of the visual cortex, specifically area IT. Moreover, other data suggest that these same visual areas are not sensitive to the affective significance of objects (Iwai et al., 1990; Nishijo, Ono, & Nishino, 1988; Rolls, 1999; Rolls, Judge, & Sanghera, 1977). Thus, within area IT and other later stages of the visual cortex we appear to have considerable evidence for categorization prior to affect retrieval.

Identification

Identification involves two distinct events. First, the brain must respond with a distinct neural signature to each specific object. Second, the brain must be able to give the *same* neural signature to multiple views of the same object regardless of orientation or distance. For exam-

ple, identification happens when there is (a) a distinct neural code for the Sears Tower (vs. other buildings or objects) and (b) the neural code for the Sears Tower is the same regardless of the size (e.g., regardless of whether we are viewing a picture or the actual building), the angle one views the Sears Tower (e.g., whether the building is viewed from the street or from an airplane), amount of lighting (e.g., whether it is day or night), and so forth. Together, we use the term *object invariance* to refer to these achievements by higher areas of the visual cortex.

Object invariance appears to be an achievement of area IT (Rolls, 1999; Vogels & Orban, 1996; Vuilleumier et al., 2002). Studies using single cell recordings have suggested that in area IT there is a unique neural population that fires for each specific stimulus shown (Rolls, 1999; Vogels & Orban, 1996). Moreover, studies using fMRI analyses with humans have found areas of the visual cortex that show a reduction of activity for repeated stimuli even when such stimuli are varied in terms of size and spatial-visual angle. Thus, despite variations in perceptual aspects, specific areas of area IT appear to treat the object identically (Dehaene et al., 2004; Grill-Spector et al., 1999; Vuilleumier et al., 2002). Object invariance has also been demonstrated with subliminal presentations of stimuli (Dehaene et al., 2001; 2004). In sum, area IT appears to create an object-invariant code for stimuli, an achievement that should be viewed in terms of identification processes.

Other imaging data suggest that area IT plays a key role in stimulus identification regardless of whether the stimuli involve words (Petersen, Fox, Snyder, & Raichle, 1990; Wiggs, Weisberg, & Martin, 1999), faces (Gorno-Tempini et al., 1998), or other pictorial stimuli (Martin et al., 1996; Vandenberghe, Price, Wise, Josephs, & Frackowiak, 1996). Therefore, although the perceptual features of stimuli do contribute to the neural organization of semantic knowledge, it is also true that area IT responds to nonperceptual aspects of similarity, and does so concerning a wide range of perceptual objects. Given this mass of data, it appears that area IT is the site and locus of invariant neural codes and therefore the site and locus of object identification processes.

Faces, which may be evolutionarily important, do appear to receive some special process-

ing by the visual cortex, as evidenced by case studies of prosopagnosia as well as imaging studies (see Duchaine & Nakayama, 2005; Kanwisher, 2000; however, see Gauthier et al., 1999, for a critical review of this point). In particular, there appear to be two distinct areas dedicated to face, one for identity (i.e., Jim's face) and one for expression (e.g., a face with raised eyebrows and wide-open eyes). Single cell recording in monkeys have identified that area STS was sensitive to facial expressions (e.g., calm vs. angry), whereas area IT was sensitive only to the facial identity (e.g., Coco v. Kiki) (Hasselmo, Rolls, & Baylis, 1989; Narumoto, Okada, Sadato, Fukui, & Yonekura, 2001). With respect to humans, imaging technology has shown a similar pattern of findings (Kanwisher, McDermott, & Chun, 1997; Rotshstein, Malach, Hadar, Graif, & Hendler, 2001). The research in total suggests that different neuron populations within the visual cortex may code for identity and expression, but that both of these achievements are prior to the retrieval of affect (Rotshstein et al., 2001).

Recall that studies have found distinct category-related ERPs within 70–80 ms poststimulus onset (e.g., Van Rullen & Thorpe, 2001). Object identification also appears to occur rapidly, perhaps within 100 ms of stimulus onset (Lehky, 2000; Rolls & Tovee, 1994). These findings suggest that categorization tends to occur prior to identification. Nevertheless, studies that present masked stimuli have demonstrated that even stimuli presented as briefly as 20–60 ms with pre- and postmasks are still sufficiently processed by area IT to support object identification (Dehaene et al., 2001, 2004; Rolls, 1999; Vogels & Orban, 1996). In the latter connection, Rolls, Tovee, Purcell, Stewart, and Azzopardi (1994) argued that such subliminal presentations reduce the amplitude of neural responses to stimuli, but do not change fundamental neural identification processes (see also Kovacs, Vogels, & Orban, 1995, for similar results). Thus, the primary difference between subliminal and optimal viewing conditions pertains to the amplitude of the neuronal responses within area IT, but sufficient processing still occurs to produce an invariant neural code (i.e., identification). From this perspective, demonstrations of “unconscious” cognition or affect are not particularly special from a neurological point of view.

Affective Encoding Is Dependent Upon Semantic Processing Activity

Cognition and Meaning

It is useful at this point to summarize our arguments so far as well as to anticipate some important questions. We wish to make clear about what we think is (and is not) happening in area IT. We also wish to clarify the relation of this neural activity to cognition and meaning, sidestepping issues (such as the nature of consciousness or brain/mind relations) that continue to be thorny within the recent neuroscience literature (e.g., Gazzaniga, 2000).

Categorization and identification are crucial semantic tasks. The evidence (as reviewed above) suggests that these processes occur in the higher areas of the visual cortex, particularly in area IT. Does this mean that we are conscious of such neural activity? No, but semantic analysis should not be equated with consciousness (Lazarus, 1995). A good deal of, if not most, semantic analysis is unconscious (Kihlstrom, 1999; Nisbett & Wilson, 1977). Does this mean that area IT “knows” what an object is? Yes. There is a distinct and invariant neural representation for that object. This means that the object has been identified. Does this mean that area IT can represent the psychological significance of the object? No. Area IT creates an invariant code for each object. It then sends the code forward within the brain to elicit memory and emotion-based associations. Although area IT knows what an object is, it does not know the object's goal-related significance. However, identifying an object is a necessary prerequisite for evaluating its significance.

Studies of Structure and Function

Although area IT can categorize and identify stimuli, it cannot evaluate their affective significance (Iwai, et al., 1990; Nishijo et al., 1988; Rolls, 1999). Once area IT identifies an image, it sends the neural code to other areas of the brain such as the amygdala, the prefrontal cortex, and the orbitofrontal cortex (among many other areas). The amygdala has been shown to be important to affective processing and has been implicated in a multitude of processes such as those related to fear conditioning, memory consolidation, face processing, attention alloca-

tion, and emotional memory (see Aggleton, 2000 for a review). Some have claimed that the amygdala is important for making evaluations of objects and that these evaluations may often precede semantic analysis (Bargh, 1997; Murphy & Zajonc, 1993; Zajonc, 2000). As this section and later sections will document, this seems unlikely.

We argue, as others have (Fukuda, Ono, & Nakamura, 1987; Nishijo et al., 1988; Rolls, 1999), that semantic analysis, as performed by area IT, is necessary in order for the amygdala to determine the affective significance of the object. Fukuda et al. (1987) tested this by temporarily impairing efficient processing within area IT. After area IT was made inactive by synaptic cooling, these investigators demonstrated that monkeys became deficient at choosing rewarding (e.g., bananas) from nonrewarding (e.g., baseballs) objects. However, the controls were quite proficient on the same task. Overall, these findings suggest that area IT provides the object-specific neural code used by the amygdala to code for affective significance.

Furthermore, single cell recordings have confirmed that, if area IT is damaged, then cells within the amygdala are less able to discriminate food objects from nonfood objects given relevant visual input (Fukuda et al., 1987; see also Easton, & Gaffan, 2002; Fukuda & Ono, 1993, for similar findings). Single-neuron recordings in the human amygdala have also found that output from area IT is critical for the amygdala to respond to affectively significant stimuli (Kreiman, Fried, & Koch, 2002). Such studies have shown that when area IT is impaired, the amygdala no longer shows activation in response to valenced objects. Such findings would seem to argue against a low route to the amygdala, particularly for complex images. Thus, these data also suggest that the amygdala, for primates, is dependent on output from the visual cortex (e.g., area IT).

Neuroclinical evidence from humans likewise indicates the reliance of the amygdala on output from area IT. Particularly good evidence for this point comes from patient LF, who lost connections from area IT to the amygdala (see Bauer, 1984). As a result, two specific deficits became apparent: (a) he developed an inability to recognize faces; and (b) he lost the ability to become aroused by visual stimuli (Bauer, 1984; Greve & Bauer, 1990). Although visual images

of nude females did not excite him, auditory erotic narratives did. This suggests that, when information from the visual cortex cannot reach the amygdala, affective analysis is impaired, thus precluding LF from seeing nude females as appetitive.

In sum, the amygdala seems to be dependent on area IT, whereas there seems to be no direct evidence for the amygdala being critical to the categorization, identification, or recognition of stimuli. These results would seem to favor the idea that semantic processing precedes affect retrieval in visual processing.

The Direct Low Route and Its Functional Capacities

LeDoux (1996) has argued for a low-route to emotion that does not require cortical involvement. For example, LeDoux, Romanski, and Xagoraris (1989) demonstrated that when rats had their visual cortex lesioned, this did not impair learning that a light would predict a shock. This suggests that the visual cortex is not necessary for visual stimuli to elicit affective reactions (i.e., fear-associated behavior). In one sense this is true, but in another sense it is not. The stimuli used in the LeDoux et al., (1989) study involved the presence or absence of light (light = CS+; dark = CS-). Such a design is not relevant to the behavioral data that is typically taken as support for the affective primacy hypothesis among humans. Specifically, the human behavioral data typically involve more complex stimuli (e.g., words, ideograms, faces) that need to be distinguished from one another.

In the latter case, when one stimulus (CS+) needs to be discriminated from another (CS-), cortical processing appears to be necessary (Duvel, Smith, Talk, & Gabriel, 2001; Jarrell, Gentile, Romanski, McCabe, & Schneiderman, 1987; Komura, Tamura, Uwano, Nishijo, Kaga, and Ono, 2001). Related experiments suggest that a sensory cortex (e.g., auditory, visual) is needed to learn associations between two related stimuli (e.g., a high vs. a low frequency tone) (Duvel et al., 2001; McCabe, McEchron, Green, & Schneiderman, 1993). Also, when associations between two stimuli (light and tone) need to be formed to predict a CS+, cortical areas appear to be necessary (Johnson & Thompson, 1969; Nicholson & Freeman, 2000). These facts severely limit the achievements of

the low route and, in turn, severely limit the relevance of this low route to everyday emotional reactions, especially among humans (Dolan, 2000; Rolls, 1999; Shi & Davis, 2001).

The preponderance of evidence thus suggests that the direct thalamus-to-amygdala pathway championed by LeDoux et al. (1989), and subsequently by Murphy and Zajonc (1993) likely plays a small to nonexistent role in most learning situations in which distinct responses are paired with distinct stimuli. The same conclusion applies to the second subcortical route involving the extrageniculate thalamo-cortico circuit (e.g., Dolan & Vuilleumier, 2003). Because human emotional reactions are almost always predicated on the nature of the emotional stimulus (e.g., a loved one, a snake), we suggest that subcortical routes may play a rather minimal role in human emotional reactions (see Rolls, 1999, for similar arguments). Certainly, LeDoux's (1996) subcortical route, if it does exist among humans (see Dolan, 2000, and Kudo, Glendenning, Frost, & Masterson, 1986, for important questions in this regard), cannot be the same ubiquitous unconscious evaluator proposed by Bargh (1997) and Zajonc (2000).

Affective Primacy Paradigms

Thus far in our review, we have suggested that semantic analysis precedes affective retrieval based on neuroscience evidence. We concluded that available evidence tends to support the idea that important aspects of categorization and identification occur in the visual cortex prior to the retrieval of affective associations. Moreover, we also concluded that affective processing relies on the categorization and identification activities associated with area IT such that, without it, affective processing does not tend to occur.

In the final major portion of the paper, we outline how some of the most important paradigms seen as supportive evidence for affective primacy might work from a neurological point of view. Here, we will focus on the mere exposure and affective priming effects, each of which has received a good deal of attention. We will argue that the findings, in each case, likely require processing by later stages of the visual cortex, which is centrally concerned with the categorization and identification of the stimulus. If this is true, the phenomena are consistent with

the idea that semantic processing is required before affective associations can be retrieved. It is important to note that we are not seeking to provide comprehensive models of these two automatic affect phenomena. Rather, we merely intend to show that such phenomena are amenable to the present analysis.

Mere Exposure

The affective primacy hypothesis rose to prominence in the early 1980s with Kunst-Wilson and Zajonc' (1980) "mere exposure" effect demonstrating that participants prefer repeated, relative to novel, stimuli even when the repetition of stimuli occurred outside of awareness. Zajonc (1980, 2000) used these findings, as well as others, to argue that affective preferences are independent of, and precede, a semantic analysis of the stimulus. Hundreds of subsequent studies replicated the mere exposure effect (Bornstein, 1989), although the precise mechanisms for the effect are still uncertain (Whittlesea & Price, 2001; Winkielman, Schwarz, Fazendeiro, & Reber, 2003).

A prominent explanation for the mere exposure effect relies on the notion that repeated events are processed more fluently. Fluency can be the product of both perceptual (Jacoby, 1983, see also, Winkielman et al., 2003) and conceptual (Whittlesea & Price, 2001, see also, Winkielman et al., 2003) factors. Winkielman et al. (2003) argued that fluency is nonsemantic in nature and, therefore, that fluency/liking relationships support Zajonc's (1980) notion that "preferences need no inferences." In the present review, we will make the case that fluency is indeed the likely variable responsible for the mere exposure effect, much as Winkielman et al. (2003) proposed. Unlike Winkielman et al. (2003), we will make the case that fluency is a result of semantic, rather than nonsemantic, processing activity. Distinguishing old versus new stimuli requires capacities related to categorization and identification and builds on the achievements of later stages of processing within the visual cortex.

Novelty Detection

Single cell recordings have shown that area IT responds to the novelty of the stimulus. With rats as subjects, Zhu and Brown (1995) found

that cells in area TE and PR were the first areas to distinguish repeated from novel stimuli, specifically by reducing their firing rate in response to repeated stimuli. This occurred even after a single presentation of an object. In addition, the activity of PR was related to the novelty of objects, whereas the activity of the hippocampus was related to the novelty of the environment (see also Zhu, McCabe, Aggleton, & Brown, 1997). These specific changes in cell activity suggest that area IT is coding for familiarity and novelty (Brown & Bashir, 2002).

A study by Fried, MacDonald, and Wilson (1997) demonstrated the manner in which the association cortices distinguish between facial expressions on the one hand and facial novelty (i.e., new faces) on the other. Fried et al. (1997) recorded cell activity in the amygdala, hippocampus and entorhinal cortex (EC). They found that the EC responds differentially on the basis of facial expressions and stimulus novelty. By contrast, the amygdala responds on the basis of facial expressions, but not on the basis of stimulus novelty (at least in the Fried et al., 1997, study). Such data point to the causal priority of visual cortical areas, which code facial identity before the valence of facial expressions (Fried et al., 1997).

Similar findings characterize novelty processing among humans. Fischer, Furmark, Wik, and Fredrikson (2000) measured rCBF in the amygdala, hippocampus, and visual cortex. They found that when movies (presenting either a park scene or a snake) were repeated, rCBF activity decreased in the amygdala, hippocampus, and later areas of the visual cortex, suggesting that all of these areas are affected by the novelty of the stimulus. Vuilleumier et al. (2002) also found that the visual cortex codes both for a view-dependent (right fusiform gyrus) and view-independent (left fusiform gyrus) repetition of stimuli. Of particular importance here, seeing the same person's face from different visual viewpoints elicits a reduction in neural activity, indicating facial identification. Furthermore, the visual cortex area termed LOC decreased activity for both real and nonreal objects, suggesting familiarity coding even for nonsense figures. Therefore, the Vuilleumier et al. study (2002) provides evidence to suggest that the visual system not only encodes whether an object is novel or not, but also can generalize stimulus familiarity to various views and visual-

spatial alterations of the stimulus. These studies provide suggestive, but not definitive, evidence for the idea that the mere exposure phenomenon is built on processing achievements within the visual cortex.

The Mere Exposure Effect and Its Neurological Basis

Lesion and clinical studies among humans have given us a better idea of how the mere exposure effect occurs. A relevant case study is of patient LF, who lost connections between his visual cortex and the limbic system (e.g., the amygdala). Despite this lesioned path, LF demonstrates the mere exposure phenomenon to visual stimuli (Greve & Bauer, 1990). This data strongly suggests that the mere exposure effect is dependent on the activity of the visual cortex, but is not dependent on the activity of the amygdala (and specifically its connections with the visual cortex).

If the mere exposure effect is built upon processing changes within the visual cortex, it is still not clear how such changes in processing enhance the likability of the stimulus. However, recent studies have provided some clues. A study by Elliott and Dolan (1998) had participants perform the mere exposure task while being scanned. Replicating typical behavioral results, participants preferred stimuli that had been subliminally presented during an earlier phase of the study, although their explicit memory performance was at chance level. The authors then contrasted areas of the brain that were active during the preference judgment task versus the explicit memory task. The preference judgment condition was marked by more activity within a number of visual processing areas (e.g., pulvinar, right superior temporal gyrus, and right fusiform gyrus), relative to the explicit memory condition. Furthermore, novel (vs. repeated) items produced enhanced activation in visual areas (left superior temporal gyrus and left fusiform gyrus) and the hippocampus. No specific activation was found for the amygdala, even within the preference condition. The authors suggested that the study provided positive evidence for the idea that mere exposure preferences emerge from processing within the medial anterior frontal region. The role of the medial anterior frontal region in mere exposure preferences is plausible as other evidence indi-

cates that the same brain region is involved in other types of preferences (Petrides, Alivisatos, Evans, & Meyer, 1993) as well as emotion judgments (Lane, Fink, Chua, & Dolan, 1997).

Clearly, more evidence on the neural basis of the mere exposure effect would be desirable. However, from existing research, it seems fairly likely that the visual cortex plays the crucial initial role in the phenomenon. The visual cortex responds differentially to objects based on their prior frequency of exposure, which establishes the initial neural signal likely involved in the mere exposure effect, regardless of whether the stimuli are presented subliminally or supra-lingually (Dehaene et al., 2001; 2004; Rolls, 1999). We suggest that this is another case in which semantic analysis by the visual cortex precedes affect, particularly because repetition priming within the visual cortex necessarily involves an implicit recognition of the stimulus as old or new. Beyond this initial basis for mere exposure preferences, subsequent neural events are somewhat sketchy. However, they tend to suggest that the mere exposure phenomenon depends on activity within frontal regions of the brain (e.g., the medial anterior frontal region) rather than on activity within the amygdala (as proposed by Zajonc, 2000).

Affective Priming

According to Bargh (1997), evidence suggests that all objects are evaluated automatically and that such evaluations precede categorization and identification. More specifically, Bargh (1997) argues the following: (a) An evaluation module exists that first evaluates every stimulus as good or bad; (b) This crude valence distinction precedes more discriminative processing (also Murphy & Zajonc, 1993); and (c) Affective reactions influence evaluations automatically without mediation by consciousness or choice. Bargh (1997) also claims that this evaluation module could be the amygdala.

In supporting aspects of this view of automatic attitudes, variants of the affective priming paradigm (Fazio, Sanbonmatsu, Powell, & Kardes, 1986) have been crucial. Affective priming occurs when briefly exposed and irrelevant primes influence how quickly a subsequent target can be evaluated, pronounced, or categorized. More specifically, affective priming is said to occur when good targets are fa-

cilitated when preceded by good (vs. bad) primes, whereas the reverse occurs for bad targets. Although a variety of studies have found affective priming, a variety of studies have not (see Klauer & Musch, 2003, for a review). Surely the phenomenon is genuine, in that it has been replicated in a number of studies, but the phenomenon often appears more fragile than the semantic priming effect (Klauer & Musch, 2003; Neely, 1991; see Storbeck & Robinson, 2004, for an empirical comparison). In addition, the operative mechanisms for affective priming are uncertain (Fazio, 2001; Klauer & Musch, 2003; Storbeck & Robinson, 2004). Our goal here is not to suggest how affective priming occurs, or to deal comprehensively with the nuances of this data, but rather to suggest how affective priming phenomena may be instantiated within the brain.

Given that the amygdala is thought to be important for learning affective associations (LeDoux, 2000), it is tempting to propose that it may also be the site and cause of affective priming specifically as well as unconscious affect more generally (Bargh, 1997). Such a proposal would seem to require that affective words are processed using different brain structures than nonaffective words. Is this plausible? Recent fMRI studies speak to this question. In two recent studies, participants were scanned while passively viewing valenced and neutral words. There was no significant amygdala activation in either study (Beauregard et al., 1997; Canli, Desmond, Zhao, Glover, and Gabrieli, 1998). However, the studies did find that frontal regions of the brain—in particular, the orbitofrontal cortex—were differentially activated by emotional words.

A recent study by Tabert et al. (2001) found that the amygdala was activated for unpleasant words, but only when people were explicitly asked to make conscious evaluations. In addition, Adolphs, Russell, and Tranel (1999) observed that a woman with bilateral damage to the amygdala could evaluate the valence of sentences, but could not correctly interpret the importance (i.e., emotional arousal) of sentences. Such evidence suggests that the amygdala is not necessary for evaluations of lexical stimuli.

To further determine the role of the amygdala in priming, Luo et al., (2004) performed a subliminal affective priming task in combination with concurrent brain scanning. They failed to

find increased activation for negative and positive words in the amygdala, relative to neutral words, even though the study did demonstrate affect-dependent repetition priming. The repetition priming appeared to be mediated by the visual word form area (VWFA), which also plays a broad role in repetition-induced fluency (i.e., for nonaffective as well as affective objects). Given the absence of amygdala activation for affective primes, in combination with the neural basis of the repetition priming effect, the results in total appear to suggest that affective priming may be dependent on the higher visual areas that support semantic priming. Such a conclusion that would be consistent with recent behavioral data (Storbeck & Robinson, 2004) as well as our prior review of the mere exposure effect.

Concerning pictorial stimuli rather than words, the evidence is more scattered and inconsistent. In tasks involving the explicit recognition of emotional faces (relative to neutral faces), amygdala activation typically does not occur (Critchley et al., 2000; Keightley et al., 2003). However, when participants are engaged in tasks in which evaluation is not the explicit focus (e.g., categorizing faces by gender), there are studies finding increased amygdala activation for fearful relative to emotionally neutral faces (Critchley et al., 2000; Morris et al., 1998; Whalen, Rauch, Etcoff, McInerney, Lee, & Jenike, 1998). Moreover, in similar tasks when processing happy or angry expressions, the amygdala does not respond or it may even decrease its activation level (Blair, Morris, Frith, Perrett, & Dolan, 1999; Morris et al., 1998). Based on this data, it is clear that the amygdala responds specifically to certain classes of stimuli (e.g., fearful faces) and is not involved in evaluating all faces. With respect to other sorts of pictures besides faces, the amygdala is recruited during explicit judgments, but typically not during nonevaluative tasks (Keightley et al., 2003; Lane, Chua, & Dolan, 1999).

Overall, it seems that findings supportive of amygdala involvement implicate stimulus arousal to a greater extent than stimulus valence. In this connection, studies that have orthogonally manipulated the arousal and valence of emotional faces (e.g., depicting fear) have suggested that amygdala activity is more correlated with the arousal dimension than with stimulus valence (Adolphs et al., 1999; Lane et al.,

1999; Morris et al., 1998). This is broadly consistent with other studies involving words (Adolphs et al., 1999; Canli et al., 1998), faces (Adolphs et al., 1999; Morris et al., 1998), and memory modulation for emotional events (Cahill, 2000). These results suggest that the amygdala may play a specific role in monitoring stimulus arousal, but it does not appear to be necessary for stimulus evaluation.

An important study by Pessoa, Kastner, and Ungerleider (2002) recapitulates some of the above points. Pessoa et al. (2002) presented neutral, positive, and negative faces to participants while they performed a gender discrimination task as well as a demanding concurrent shape discrimination task. Participants were scanned during task performance. In the gender discrimination condition, in which attentional resources were still available, the amygdala responded differentially to fearful faces versus neutral ones. However, in the demanding attention condition, the amygdala failed to respond differentially to fearful faces versus neutral ones. The authors concluded that amygdala-related processing of fearful stimuli is driven by top-down fronto-parietal attention networks. If this is true, the amygdala does not automatically process emotional information at all, but rather is dependent on a certain level of focal attention (i.e., input from fronto-parietal networks). Such data again suggest that the amygdala does not automatically evaluate stimuli without wider occipital, parietal, and frontal input.

Given these considerations, we suggest that the amygdala is not a ubiquitous seat of evaluation, but rather that evaluation depends upon a distributed network that includes the amygdala, orbitofrontal cortex, anterior cingulate, insula, and prefrontal cortical areas, among other areas. More critically, we would suggest that the role of the amygdala is more concerned with assessing the affective significance of objects (and thus its role in responding to stimulus arousal) rather than their valence. However, it appears that the amygdala can be recruited to evaluate whether images or words are pleasant or unpleasant, specifically by more frontal cortical areas (Beauregard et al., 1997; Tabert et al., 2001). In sum, affective priming appears to be a result of complex pattern of processing that involves multiple neurological systems, including higher order areas of the visual cortex (e.g., VWFA). The latter conclusion is very much

inconsistent with an obligatory low route to affective evaluation.

Conclusion

Issues concerning cognitive versus affective primacy are often discussed at an abstract, theoretical level. For this reason, it is helpful to recast the debate in terms of a metaphor that is more concrete. Imagine that our protagonist, Jim, is walking through a National Park with his friendly companion Rover. Although Jim's goal is simply to enjoy the surroundings, it is surely important to pay heed to unsuspected dangers (wolves, snakes, bears, etc.). Data are consistent with the idea that people can unconsciously evaluate threats (Öhman, 1997). However, would it be adaptive for Jim to learn that an object is "bad" without knowing what the object is? We do not think so. A bunny rabbit is bad because it chews on our cherished plants; poison oak is bad because it causes us to itch; a mosquito is bad because it injects poison and buzzes annoyingly, and so forth. A grizzly bear is bad for quite a different reason (i.e., it is dangerous). Simply knowing that an object is "bad" would give Jim no useful information. Should Jim run (bear), freeze (snake), watch one's step (poison oak), or swat at it (mosquito)? Note in particular that diametrically opposed actions are required for the mosquito and the bear: While swatting at a mosquito is useful, swatting at a bear is not. In short, affect without identification is relatively useless in guiding one's actions (see also Barrett, Gross, Christensen, & Benvenuto, 2001).

It is important to note that, in our discussion of Jim's walk through the woods, we do not make any assumptions about conscious versus unconscious processes. Important aspects of categorization and identification occur unconsciously. For this reason, it is quite possible to have affective preferences without conscious knowledge of what an object is (as suggested by Zajonc, 1980). However, it is not possible to have affective preferences without a certain degree of preconscious categorization. In this respect, we are in agreement with the statement made by Rolls (1999), as quoted at the beginning of the introduction. Simply put, the visual system is not set up to detect affect, but rather to identify objects in order for correct affective associations to be retrieved.

In closing, we agree with Arnold (1960) and Zajonc (1980), as well as many others, that affect is often computed on a preconscious basis. For this reason, we are often surprised by our emotions (see Clore, 1994) and often cannot articulate a clear rationale for our feelings (Haidt, 2001). However, issues of consciousness are ultimately not very productive in siding in favor of affective (Zajonc, 1980) or cognitive (Lazarus, 1995) primacy, precisely because both sorts of operations are frequently, if not typically, unconscious (Kihlstrom, Mulvaney, Tobias, & Tobis, 2000). Our review of available neurological data, nevertheless, provided relatively conclusive data in favor of cognitive primacy as (a) affective categorization does not take place within the visual cortex (e.g., Rolls, 1999) and (b) categorization and identification does take place within the visual cortex (e.g., Mishkin, Ungerleider, & Macko, 2000). Our review suggests that cognition is primary to affect, both in causal and temporal terms.

References

- Adolphs, R., Russell, J., & Tranel, D. (1999). A role for the human amygdala in recognizing emotional arousal from unpleasant stimuli. *Psychological Science, 10*, 167–171.
- Aggleton, J. (2000). *The Amygdala: A Functional Analysis*. Oxford, UK: Oxford University Press.
- Arnold, M. (1960). *Emotion and personality: Neurological and physiological aspects, Vol. 2*. New York: Columbia University Press.
- Bargh, J. (1997). The automaticity of everyday life. In R. S. Wyer Jr. (Ed.), *The automaticity of everyday life: Advances in social cognition, Vol. 10* (pp. 1–61). Mahwah, NJ: Erlbaum.
- Barrett, L. F., Gross, J., Christensen, T., & Benvenuto, M. (2001). Knowing what you're feeling and knowing what to do about it: Mapping the relation between emotion differentiation and emotion regulation. *Cognition & Emotion, 15*, 713–724.
- Bauer, R. (1984). Autonomic recognition of names and faces in prosopagnosia: A neuropsychological application of the guilty knowledge test. *Neuropsychologia, 22*, 457–469.
- Beauregard, M., Chertkow, H., Bub, D., Murtha, S., Dixon, R., & Evans, A. (1997). The neural substrate for concrete, abstract, and emotional word lexica: A positron emission tomography study. *Journal of Cognitive Neuroscience, 9*, 441–461.
- Blair, R., Morris, J., Frith, C., Perrett, D., & Dolan, R. (1999). Dissociable neural responses to facial

- expressions of sadness and anger. *Brain*, *122*, 883–893.
- Bornstein, R. (1989). Exposure and affect: Overview and meta-analysis of research, 1968–1987. *Psychological Bulletin*, *106*, 265–289.
- Brown, M., & Bashir, Z. (2002). Evidence concerning how neurons of the perirhinal cortex may effect familiarity discrimination. *Philosophical Transactions of the Royal Society of London—Series B: Biological Sciences*, *357*, 1083–1095.
- Cahill, L. (2000). Modulation of long-term memory in humans by emotional arousal: Adrenergic activation and the amygdala. In J. P. Aggleton (Ed.) *The amygdala: A functional analysis* (pp. 425–446). New York: Oxford University Press.
- Canli, T., Desmond, J., Zhao, Z., Glover, G., & Gabrieli, J. (1998). Hemispheric asymmetry for emotional stimuli detected with fMRI. *NeuroReport*, *9*, 3233–3239.
- Chao, L., Haxby, J., & Martin, A. (1999). Attribute-based neural substrates in temporal cortex for perceiving and knowing about objects. *Nature Neuroscience*, *2*, 913–919.
- Clore, G. L. (1994). Can emotions be nonconscious? In P. Ekman & R. Davidson (Eds.), *The Nature of Emotion: Fundamental Questions* (pp. 283–299). London: Oxford University Press.
- Clore, G. L., & Ortony, A. (2000). Cognition in emotion: Always, sometimes, or never? In R. D. Lane & L. Nadel (Eds.), *Cognitive Neuroscience of Emotion* (pp. 24–61). New York: Oxford University Press.
- Critchley, H., Daly, E., Phillips, M., Brammer, M., Bullmore, E., Williams, S., Van Amelsvoort, T., Robertson, D., David, A., & Murphy, D. (2000). Explicit and implicit neural mechanisms for processing of social information from facial expressions: A functional magnetic resonance imaging study. *Human Brain Mapping*, *9*, 93–105.
- Damasio, A. (1990). Category-related recognition defects as a clue to the neural substrates of knowledge. *Trends in Neurosciences*, *13*, 95–98.
- Damasio, H., Grabowski, T., Tranel, D., Hichwa, R., & Damasio, A. (1996). A neural basis for lexical retrieval. *Nature*, *380*, 499–505.
- Dehaene, S., Jobert, A., Naccache, L., Ciuciu, P., Poline, J., Bihan, D., & Cohen, L. (2004). Letter binding and invariant recognition of masked words: Behavioral and neuroimaging evidence. *Psychological Science*, *15*, 307–313.
- Dehaene, S., Naccache, L., Cohen, L., Bihan, D., Mangin, J., Poline, J., & Riviere, D. (2001). Cerebral mechanisms of word masking and unconscious repetition priming. *Nature Neuroscience*, *4*, 752–758.
- Dolan, R. (2000). Functional neuroimaging of the amygdala during emotional processing and learning. In J. P. Aggleton (Ed.), *The amygdala: A functional analysis* (pp. 631–654). New York: Oxford University Press.
- Dolan, R., & Vuilleumier, P. (2003). Amygdala automaticity in emotional processing. *Annals of the New York Academy of Sciences*, *985*, 348–355.
- Duchaine, B., & Nakayama, K. (2005). Dissociations of face and object recognition in developmental prosopagnosia. *Journal of Cognitive Neuroscience*, *17*, 249–261.
- Duvel, A., Smith, D., Talk, A., & Gabriel, M. (2001). Medial geniculate, amygdalar and cingulate cortical training-induced neuronal activity during discriminative avoidance learning in rabbits with auditory cortical lesions. *Journal of Neuroscience*, *21*, 3271–3281.
- Easton, A., & Gaffan, D. (2002). Insights into the nature of fronto-temporal interactions from a bi-conditional discrimination task in the monkey. *Behavioural Brain Research*, *136*, 217–226.
- Elliott, R., & Dolan, R. J. (1998). Neural response during preference and memory judgments for subliminally presented stimuli: A functional imaging study. *Journal of Neuroscience*, *18*, 4697–4704.
- Farah, M., Humphreys, G., & Rodman, H. (1999). Object and face recognition. In M. Zigmond, F. Bloom et al. (Eds.), *Fundamental neuroscience* (pp. 1339–1361). San Diego, CA: Academic Press.
- Fazio, R. (2001). On the automatic activation of associated evaluations: An overview. *Cognition & Emotion*, *15*, 115–141.
- Fazio, R., Sanbonmatsu, D., Powell, M., & Kardes, F. (1986). On the automatic activation of attitudes. *Journal of Personality and Social Psychology*, *50*, 229–238.
- Fischer, H., Furmark, T., Wik, G., & Fredrikson, M. (2000). Brain representation of habituation to repeated complex visual stimulation studied with PET. *NeuroReport*, *11*, 123–126.
- Fried, I., MacDonald, K., & Wilson, C. (1997). Single neuron activity in human hippocampus and amygdala during recognition of faces and objects. *Neuron*, *18*, 753–765.
- Fukuda, M., & Ono, T. (1993). Amygdala-hypothalamic control of feeding behavior in monkey: Single cell responses before and after reversible blockade of temporal cortex or amygdala projections. *Behavioural Brain Research*, *55*, 233–241.
- Fukuda, M., Ono, T., & Nakamura, K. (1987). Functional relations among inferiortemporal cortex, amygdala, and lateral hypothalamus in monkey operant feeding behavior. *Journal of Neurophysiology*, *57*, 1060–1077.
- Gauthier, I., Behrmann, M., & Tarr, M. J. (1999). Can face recognition really be dissociated from object recognition? *Journal of Cognitive Neuropsychology*, *11*, 349–370.

- Gazzaniga, M. (Ed.). (2000). *The new cognitive neurosciences* (2nd ed.). Cambridge, MA: The MIT Press.
- Goodale, M., & Milner, A. (1992). Separate visual pathways for perception and action. *Trends in Neurosciences*, *15*, 20–25.
- Gorno-Tempini, M., Price, C., Josephs, O., Vandenberghe, R., Cappa, S., Kapur, N., Frackowiak, R. (1998). The neural systems sustaining face and proper-name processing. *Brain*, *121*, 2103–2118.
- Greve, K., & Bauer, R. (1990). Implicit learning of new faces in prosopagnosia: An application of the mere-exposure paradigm. *Neuropsychologia*, *28*, 1035–1041.
- Grill-Spector, K., Kushnir, T., Edelman, S., Avidan, G., Itzhak, Y., & Malach, R. (1999). Differential processing of objects under various viewing conditions in the human lateral occipital complex. *Neuron*, *24*, 187–203.
- Haidt, J. (2001). The emotional dog and its rational tail: A social intuitionist approach to moral judgment. *Psychological Review*, *108*, 814–834.
- Hasselmo, M., Rolls, E. T., & Baylis, G. (1989). The role of expression and identity in the face-selective responses of neurons in the temporal visual cortex of the monkey. *Behavioural Brain Research*, *32*, 203–218.
- Herath, P., Kinomura, S., & Roland, P. (2001). Visual recognition: Evidence for two distinctive mechanisms from a PET study. *Human Brain Mapping*, *12*, 110–119.
- Herbster, A., Mintun, M., Nebes, R., & Becker, J. (1997). Regional cerebral blood flow during word and nonword reading. *Human Brain Mapping*, *5*, 84–92.
- Iwai, E., Yukie, M., Watanabe, J., Hikosaka, K., Suyama, H., & Ishikawa, S. (1990). A role of amygdala in visual perception and cognition in macaque monkeys (*macaca fuscata* and *macaca mulatta*). *Tohoku Journal of Experimental Medicine*, *161* (Suppl.), 95–120.
- Jacoby, L. (1983). Perceptual enhancement: Persistent effects of an experience. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, *9*, 21–38.
- Jarrell, T., Gentile, C., Romanski, L., McCabe, P., & Schneiderman, N. (1987). Involvement of cortical and thalamic auditory regions in retention of differential bradycardic conditioning to acoustic conditioned stimuli in rabbits. *Brain Research*, *412*, 285–294.
- Johnson, R., & Thompson, R. (1969). Role of association cortex in auditory-visual conditional learning in the cat. *Journal of Comparative and Physiological Psychology*, *69*, 485–491.
- Kanwisher, N. (2000). Domain specificity in face perception. *Nature Neuroscience*, *3*, 759–763.
- Kanwisher, N., McDermott, J., & Chun, M. (1997). The fusiform face area: A module in human extrastriate cortex specialized for face perception. *Journal of Neuroscience*, *17*, 4302–4311.
- Keightley, M., Winocur, G., Graham, S., Mayberg, H., Hevenor, S., & Grady, C. (2003). An fMRI study investigating cognitive modulation of brain regions associated with emotional processing of visual stimuli. *Neuropsychologia*, *41*, 585–596.
- Kihlstrom, J. (1999). The psychological unconscious. In L. A. Pervin & O. P. John (Eds.), *Handbook of personality: Theory and research* (2nd ed., pp. 424–442). New York: Guilford Press.
- Kihlstrom, J., Mulvaney, S., Tobias, B., & Tobis, I. (2000). The emotional unconscious. In E. Eich, J. Kihlstrom, et al. (Eds.), *Cognition and emotion* (pp. 30–86). London, UK: Oxford University Press.
- Klauer, K. C., & Musch, J. (2003). Affective priming: Findings and theories. In J. Musch & K. C. Klauer (Eds.), *The Psychology of Evaluation: Affective Processes in Cognition and Emotion* (pp. 7–49). Mahwah, NJ: Erlbaum.
- Komura, Y., Tamura, R., Uwano, T., Nishijo, H., Kaga, K., & Ono, T. (2001). Retrospective and prospective coding for predicted reward in the sensory thalamus. *Nature*, *412*, 546–549.
- Kovacs, G., Vogels, R., & Orban, G. (1995). Cortical correlate of pattern backward masking. *Proceedings of the National Academy of Sciences, USA*, *92*, 5587–5591.
- Kreiman, G., Fried, I., & Koch, C. (2002). Single-neuron correlates of subjective vision in the human medial temporal lobe. *Proceedings of the National Academy of Sciences, USA*, *99*, 8378–8383.
- Kudo, M., Glendenning, K., Frost, S., & Masterson, R. (1986). Origin of mammalian thalamocortical projections. I. Telencephalic projection of the medial geniculate body in the opossum (*Didelphis virginiana*). *Journal of Comparative Neurology*, *245*, 176–197.
- Kunst-Wilson, W., & Zajonc, R. (1980, February 1). Affective discrimination of stimuli that cannot be recognized. *Science*, *207*, 557–558.
- Lane, R., Chua, P., & Dolan, R. (1999). Common effects of emotional valence, arousal and attention on neural activation during visual processing of pictures. *Neuropsychologia*, *37*, 989–997.
- Lane, R., Fink, G., Chua, P., & Dolan, R. J. (1997). Neural activation during selective attention to subjective emotional responses. *NeuroReport*, *8*, 3969–3972.
- Lazarus, R. (1984). On the primacy of cognition. *American Psychologist*, *39*, 124–129.
- Lazarus, R. (1995). Vexing research problems inherent in cognitive-mediational theories of emotion and some solutions. *Psychological Inquiry*, *6*, 183–196.

- LeDoux, J. (1996). *The emotional brain: The mysterious underpinnings of emotional life*. New York: Simon & Schuster.
- LeDoux, J. (2000). Cognitive-emotional interactions: Listen to the brain. In R. Lane & L. Nadel (Eds.), *Cognitive neuroscience of emotion. Series in affective science* (pp. 129–155). New York: Oxford University Press.
- LeDoux, J., Romanski, L., & Xagoraris, A. (1989). Indelibility of subcortical emotional memories. *Journal of Cognitive Neuroscience, 1*, 238–243.
- Lee, A., Graham, K., Simons, J., Hodges, J., Owen, A., & Patterson, K. (2002). Regional brain activations differ for semantic features but not categories. *Neuroreport, 13*, 1497–1501.
- Lehky, S. (2000). Fine discrimination of faces can be performed rapidly. *Journal of Cognitive Neuroscience, 12*, 848–855.
- Leventhal, H., & Scherer, K. (1987). The relationship of emotion to cognition: A functional approach to a semantic controversy. *Cognition & Emotion, 1*, 3–28.
- Luo, Q., Peng, D., Jin, Z., Xu, D., Xiao, L., & Ding, G. (2004). Emotional valence of words modulates the subliminal repetition priming effect in the left fusiform gyrus: An event-related fMRI study. *NeuroImage, 21*, 414–421.
- Martin, A., Wiggs, C., Ungerleider, L., & Haxby, J. (1996). Neural correlates of category-specific knowledge. *Nature, 379*, 649–652.
- McCabe, P., McEchron, M., Green, E., & Schneiderman, N. (1993). Electrolytic and ibotenic acid lesions of the medial subnucleus of the medial geniculate prevent the acquisition of classically conditioned heart rate to a single acoustic stimulus in rabbits. *Brain Research, 619*, 291–298.
- Mishkin, M., Ungerleider, L., & Macko, K. (2000). Object vision and spatial vision: Two cortical pathways. In S. Yantis (Ed.), *Visual perception: Essential readings* (pp. 296–302). New York: Psychology Press.
- Morris, J., Friston, K., Buchel, C., Frith, C., Young, A., Calder, A., & Dolan, R. (1998). A neuromodulatory role for the human amygdala in processing emotional facial expressions. *Brain, 121*, 47–57.
- Moscovitch, M., Winocur, G., & Behrmann, M. (1997). What is special about face recognition? Nineteen experiments on a person with visual object agnosia and dyslexia but normal face recognition. *Journal of Cognitive Neuroscience, 9*, 555–604.
- Murphy, S., & Zajonc, R. (1993). Affect, cognition, and awareness: Affective priming with optimal and suboptimal stimulus exposure. *Journal of Personality and Social Psychology, 64*, 723–739.
- Narumoto, J., Okada, T., Sadato, N., Fukui, K., & Yonekura, Y. (2001). Attention to emotion modulates fMRI activity in human right superior temporal sulcus. *Cognitive Brain Research, 12*, 225–231.
- Neely, J. (1991). Semantic priming effects in visual word recognition: A selective review of current findings and theories. In D. Besner & G. Humphreys (Eds.), *Basic processing in reading: Visual word recognition* (pp. 264–336). Hillsdale, NJ: Erlbaum.
- Nicholson, D., & Freeman, J. (2000). Lesions of the perirhinal cortex impair sensory preconditioning in rats. *Behavioural Brain Research, 112*, 69–75.
- Nisbett, R., & Wilson, T. D. (1977). Telling more than we can know: Verbal reports on mental processes. *Psychological Review, 84*, 231–259.
- Nishijo, H., Ono, T., & Nishino, H. (1988). Single neuron response in amygdala of alert monkey during complex sensory stimulation with affective significance. *Journal of Neuroscience, 8*, 3570–3583.
- Nobre, A., Allison, T., & McCarthy, G. (1994). Word recognition in the human inferior temporal lobe. *Nature, 372*, 260–263.
- Öhman, A. (1997). As fast as the blink of an eye: Evolutionary preparedness for preattentive processing of threat. In P. J. Lang, R. F. Simons et al. (Eds.), *Attention and orienting: Sensory and motivational processes* (pp. 165–184). Mahwah, NJ: Erlbaum.
- Pessoa, L., Kastner, S., & Ungerleider, L. (2002). Attentional control of the processing of neutral and emotional stimuli. *Cognitive Brain Research, 15*, 31–45.
- Petersen, S., Fox, P., Snyder, A., & Raichle, M. (1990, August 31). Activation of extrastriate and frontal cortical areas by visual words and word-like stimuli. *Science, 249*, 1041–1044.
- Petrides, M., Alivisatos, B., Evans, A., & Meyer, E. (1993). Dissociation of human mid-dorsolateral from posterior dorsolateral frontal cortex in memory processing. *Proceedings of the National Academy of Sciences, USA, 90*, 873–877.
- Price, C., Wise, R., & Frackowiak, R. (1996). Demonstrating the implicit processing of visually presented words and pseudowords. *Cerebral Cortex, 6*, 62–70.
- Puce, A., Allison, T., Asgari, M., Gore, J., & McCarthy, G. (1996). Differential sensitivity of human visual cortex to faces, letter strings, and textures: A functional magnetic resonance imaging study. *Journal of Neuroscience, 16*, 5205–5215.
- Reed, J., Squire, L., Patalano, A., Smith, E., & Jonides, J. (1999). Learning about categories that are defined by object-like stimuli despite impaired declarative memory. *Behavioral Neuroscience, 113*, 411–419.
- Robinson, M. D. (1998). Running from William James' bear: A review of preattentive mechanisms

- and their contributions to emotional experience. *Cognition and Emotion*, *12*, 667–696.
- Rolls, E. T. (1999). *The brain and emotion*. Oxford, UK: Oxford University Press.
- Rolls, E. T., Judge, S., & Sanghera, M. (1977). Activity of neurons in the inferotemporal cortex of the alert monkey. *Brain Research*, *130*, 229–238.
- Rolls, E. T., & Tovee, M. (1994). Processing speed in the cerebral cortex and the neurophysiology of visual masking. *Proceedings of the Royal Society of London Series B Biological Sciences*, *257*, 9–15.
- Rolls, E. T., Tovee, M., Purcell, D., Stewart, A., & Azzopardi, P. (1994). The responses of neurons in the temporal cortex of primates, and face identification and detection. *Experimental Brain Research*, *101*, 473–484.
- Rotshstein, P., Malach, R., Hadar, U., Graif, M., & Hendler, T. (2001). Feeling or features: Different sensitivity to emotion in high-order visual cortex and amygdala. *Neuron*, *32*, 747–757.
- Shi, C., & Davis, M. (2001). Visual pathways involved in fear conditioning measured with fear-potentiated startle: Behavioral and anatomic studies. *Journal of Neuroscience*, *21*, 9844–9855.
- Storbeck, J., & Robinson, M. D. (2004). Preferences and inferences in encoding visual objects: A systematic comparison of semantic and affective priming. *Personality and Social Psychology Bulletin*, *30*, 81–93.
- Strange, B., Henson, R., Friston, K., & Dolan, R. (2000). Brain mechanisms for detecting perceptual, semantic, and emotional deviance. *Neuroimage*, *12*, 425–433.
- Sugase, Y., Yamane, S., Ueno, S., & Kawano, K. (1999). Global and fine information coded by single neurons in the temporal visual cortex. *Nature*, *400*, 869–873.
- Tabert, M., Borod, J., Tang, C., Lange, G., Wei, T., Johnson, R., Nusbaum, A., & Buchsbaum, M. (2001). Differential amygdala activation during emotional decision and recognition memory tasks using unpleasant words: An fMRI study. *Neuropsychologia*, *39*, 556–573.
- Tranel, D., Damasio, H., & Damasio, A. (1997). A neural basis for the retrieval of conceptual knowledge. *Neuropsychologia*, *35*, 1319–1327.
- Vandenberghe, R., Price, C., Wise, R., Josephs, O., & Frackowiak, R. (1996). Functional anatomy of a common semantic system for words and pictures. *Nature*, *383*, 254–256.
- Van Rullen, R., & Thorpe, S. (2001). The time course of visual processing: From early perception to decision-making. *Journal of Cognitive Neuroscience*, *13*, 454–461.
- Vogels, R., & Orban, G. (1996). Coding of stimulus invariance by inferior temporal neurons. *Progress in Brain Research*, *112*, 195–211.
- Vuilleumier, P., Henson, R., Driver, J., & Dolan, R. (2002). Multiple levels of visual object constancy revealed by event-related fMRI of repetition priming. *Nature Neuroscience*, *5*, 491–499.
- Whalen, P., Rauch, S., Etcoff, N., McInerney, S., Lee, M., & Jenike, M. (1998). Masked presentations of emotional facial expressions modulate amygdala activity without explicit knowledge. *Journal of Neuroscience*, *18*, 411–418.
- Whittlesea, B., & Price, J. R. (2001). Implicit/explicit memory versus analytic/nonanalytic processing: Rethinking the mere exposure effect. *Memory & Cognition*, *29*, 234–246.
- Wiggs, C., Weisberg, J., & Martin, A. (1999). Neural correlates of semantic and episodic memory retrieval. *Neuropsychologia*, *37*, 103–118.
- Winkielman, P., Schwarz, N., Fazendeiro, T., & Reber, R. (2003). The hedonic marking of processing fluency: Implications for evaluative judgment. In J. Musch & K. Klauer (Eds.), *The psychology of evaluation: Affective processes in cognition and emotion* (pp. 189–217). Mahwah, NJ: Erlbaum.
- Zajonc, R. (1980). Feeling and thinking: Preferences need no inferences. *American Psychologist*, *35*, 151–175.
- Zajonc, R. (1984). On the primacy of affect. *American Psychologist*, *39*, 117–123.
- Zajonc, R. (2000). Feeling and thinking: Closing the debate over the independence of affect. In J. P. Forgas (Ed.), *Feeling and thinking: The role of affect in social cognition. Studies in emotion and social interaction, Vol. 2.* (pp. 31–58). New York: Cambridge University Press.
- Zhu, X., & Brown, M. (1995). Changes in neuronal activity related to the repetition and relative familiarity of visual stimuli in rhinal and adjacent cortex of the anaesthetised rat. *Brain Research*, *689*, 101–110.
- Zhu, X., McCabe, B., Aggleton, J., & Brown, M. (1997). Differential activation of the rat hippocampus and perirhinal cortex by novel visual stimuli and a novel environment. *Neuroscience Letters*, *229*, 141–143.

Received November 16, 2004

Revision received April 11, 2005

Accepted April 15, 2005 ■