

Conscious and Nonconscious Processing of Visual Object Identity

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Priming as implicit memory

Recognizing a perceptual stimulus improves with familiarity. This experience-specific facilitation is termed *priming*. In a typical priming experiment, subjects are initially exposed to a set of briefly presented stimuli in the prime block and their performance in naming, for example, is recorded (usually reaction times and correct responses). In a subsequent test block, subjects are presented with either the same stimuli or stimuli that have some defined relationship to the prime stimuli. Any improvement that is specific to the stimulus is taken as a measure of priming.

Priming is considered an implicit type of memory because it does not involve explicit recollection of previous experience. It is believed to exist as an independent mechanism, while closely interacting with other memory systems (Tulving & Schacter 1990). Amnesic patients, for example, can show almost intact priming while their explicit recognition memory (as measured in an old/new judgment task) has been severely impaired (Weiskrantz & Warrington 1970; Warrington & Weiskrantz 1974; Cave & Squire 1992). In other types of experiments, it has been shown that elaborating the study material improved explicit memory (e.g., measured by a cued recall of stem completions),¹ but not priming (Graf & Mandler 1984). Priming and explicit memory have also been suggested to have different retention time courses (Jacoby 1983). Priming of object naming can last 48 weeks after a single exposure to a picture (Cave 1997), and priming of word completions can even last as long as 16 months (Sloman, Hayman, Ohta, Law & Tulving 1988).

Although the contribution of priming is implicit, it has been shown to facilitate tasks that require explicit knowledge, such as object naming² (Bartram 1974; Biederman & Cooper 1991; Schacter, Delaney & Merikle 1990). The mechanisms subserving the interaction between priming and explicit reports, as manifested in object recognition, will be the focus of this chapter.

Working definitions

The terms *subliminal* and *visual awareness* are being used extensively. The following are working definitions for these concepts.

Subliminal is taken here in its literal meaning: below-threshold. The threshold is defined by the task. Therefore, if subjects are required to detect the presence or absence of a certain stimulus on the screen and they cannot do it above chance, this detection is considered to be below their threshold, and therefore subliminal. However, if the task is naming briefly presented objects, the threshold is identification. A trial in a naming task is then considered subliminal if subjects cannot name the objects, even if they are above chance in detecting their presence. The tasks of detection and naming differ largely in the information that they require for successful performance, and the thresholds are expected to be different. In addition, in light of the priming phenomenon, this threshold should not be considered as fixed but rather as a measure that can vary with experience. As demonstrated by the experimental work reviewed here, subjects could gain from subliminal presentations information that can render the same stimuli supraliminal in subsequent trials.

Work on signal detection theory (Swets 1961; Green & Swets 1966) challenges the existence of a sensory threshold. The threshold is described instead by a bell-shaped curve representing the distribution of the probability for correct performance. In the present context, "subliminal" is used to describe success (or, rather, failure) in performing the task at hand, and in that sense it is a binary concept. "Visual awareness," on the other hand, is taken to be more like a continuum, and therefore closer to the threshold definition of signal detection theory.³ If a presentation of an object is too brief for identification, it is subliminal in that subjects cannot identify it, and therefore they are unaware of the name. At the same time, however, they might be aware of other aspects of the identity, such as orientation and texture. In that sense, awareness is a set of dimensions on which a threshold may be defined.

Such "intermediate-awareness" of the identity is often hard to infer from subjects' reports. In trying to estimate the awareness of subjects with regard to different aspects of the stimulus, the experiment should be designed so that the report will be minimally affected by subjective factors. When subjects cannot name the stimulus, intermediate reports can vary significantly, and they are likely to depend on individual differences in verbal articulation, visual memory, etc. In addition, subjects can make accurate discriminations even when they believe that their knowledge is insufficient for a correct judgment (reported as early as Sidis, 1898, and more recently, Kolb & Braun 1995). Indeed, Cheesman and Merikle (1984) distinguish between "subjective-threshold," when subjects believe they are guessing while their performance is above chance, and an "objective-threshold," which is chance-level performance. Self-judgments of awareness and confidence are thus highly subjective, and should be augmented with objective measures of performance.

Subliminal perception and visual awareness

Direct tests such as recognition are likely to involve effects of both explicit and implicit processes. To distinguish their contribution, Jacoby (1991) developed the process dissociation task. He assumed that "implicit" and "nonintentional" are representing unconscious processes, and that "explicit" and "intentional" are representing conscious processes. The rationale behind Jacoby's task is that the contribution of intentional and nonintentional processes can be inferred by comparing performance between conditions in which they are acting together and conditions in which they are competing. For example, after studying a list of words, subjects were required to complete stems of words with either words from the study list (*inclusion* condition), or with words not from the study list (*exclusion* condition) (Jacoby, Toth, Yonelinas 1993). The difference in performance between the two conditions was taken to indicate an intentional retrieval, and any study items that are provided in the exclusion condition to indicate nonintentional use of memory. The results show that study words that were presented very briefly (Debnar & Jacoby 1994), or in a divided attention task⁴ (Jacoby *et al.* 1993) were given equally often on inclusion and exclusion conditions, and at a rate that was significantly higher than baseline.⁵ Therefore, under these conditions, all the priming was nonintentional.

This technique has been proven useful and is extensively used for similar assessments of conscious and unconscious effects. Other demonstrations, using various paradigms, have shown that the effect of subliminal presentations might range from the bias of judgment and affect to the facilitation of visual object recognition.

In one type of such studies (Marcel 1983; Merikle, Joordens & Stolz 1995), subjects were required to name the color of a target patch that was presented on the screen until they responded. The patch was preceded by a subliminal (individually determined for each subject) color name (e.g., 'GREEN'). Performance was affected by the congruency between the name and the color patch (Stroop effect) such that color-congruent words shortened reaction times (RTs), and color-incongruent words delayed RTs. Therefore, although the prime was not recognizable it affected responses in the subsequent naming task.

Another example is the effect of subliminal presentations on subsequent liking judgments (Zajonc 1968). In one such study (Kunst-Wilson & Zajonc 1980), subjects were first presented with irregular octagons for a very brief duration (1 ms). Then, pairs of such octagons — one new and one from the set that had been presented previously — were displayed on the screen for 1 sec. Subjects were required to: (a) choose which octagon they liked more, and (b) judge which of the two octagons they had seen before (old/new judgment). Although they were at chance in the old/new judgment task, they tended to like the old stimuli more than the new ones. Consequently, the authors concluded that the subliminal presentations only affected judgments of liking. Experiments reviewed here show that subliminal presentations can also facilitate object identification (Bar & Biederman 1998; 1999). An implication of these results is that priming of perception may be more affected by a subliminal stimulus than the explicit measure of old/new judgments.

Finally, in a recent study of subliminal semantic activation (Greenwald, Draine Abrams 1996), a prime word was presented very briefly before the presentation of above-threshold target words. Subjects were required to judge whether the target was a pleasant or unpleasant word, or whether it represented a male or female name. Their judgments were biased by the subliminal prime. For example, a prime word "kill" biased judgments of a target word "bomb" towards unpleasantness, while a prime word "happy" biased the judgment of the same word towards pleasantness. This subliminal priming, which was purely semantic (as the prime and the target were different words

that could only be semantically related), has been found to be very short-lived: the target word had to be presented within 100 ms following the prime in order to obtain the effect. Subliminal visual priming, on the other hand, is suggested later to persist for longer durations. Therefore, this ephemeral nature might be unique to subliminal semantic priming.

We turn now from studies of subliminal priming to consider the related issue of visual awareness. While studying visual awareness in general has a long history, the underlying neural mechanisms have been addressed only recently. Two related phenomena that have been studied extensively are *blindsight* and *binocular rivalry*.

Blindsight is the ability of patients with a damaged primary visual cortex (or the projections to it) to report aspects of a stimulus that is presented to the blind area of their visual field (Weiskrantz 1986). Such patients perform reliably above chance (typically in localization tasks), often despite their low confidence in their response. Blindsight may thus be considered as an example of perception without awareness.

Experimental methods have been devised to induce behavior similar to blindsight in healthy human observers (Meeres & Graves 1990; Kolb & Braun 1995). For example, when subjects had to locate an open circle that was presented very briefly in one of six possible positions (Meeres & Graves 1990), they were significantly better than chance in guessing its location, even when they reported that the circle was absent. In such studies, however, the relation between subjective confidence judgments and awareness is not completely defined.

The capacity of blindsight is likely mediated by alternative connections to other areas. Hypotheses regarding the anatomical basis of blindsight include the retinocollicular pathway (i.e., the pathway from the retina to the superior colliculus), the direct projections from the thalamus to extrastriate cortex, and residual projections that survived the damage (Stoerig 1993). Each patient might have a different type of damage, and therefore blindsight might have different substrates in each instance. The important common aspect is subjects' ability to perform successfully in spite of their low confidence.

Findings from studies of form-agnosia further extend the blindsight phenomenon. One striking example is patient D. F. (Milner & Goodale 1995), who has suffered damage to her visual cortex following carbon monoxide intoxication. While visual areas V2, V3 were severely damaged, area V1 remained mostly intact. D.F. is unable to recognize familiar faces, line draw-

ings of objects, or even simple geometric shapes. She also cannot discriminate between objects that differ in size or orientation. Her basic visual abilities (e.g., contrast sensitivity, visual field), however, are relatively intact. In one study (Goodale, Meenan, Bühlhoff, Nicolle, Murphy & Racicot 1994), D.F. was required both to discriminate between blob-like wooden objects (same/different task), and grasp them using shape information. Although she failed to discriminate between the shapes, she had no difficulty in choosing stable grasping points on the circumference of the object. These results suggest that D.F. could match her grasping points to the specific object form without being aware of its shape.

Another class of studies related to visual awareness is binocular rivalry. When the two eyes are presented with conflicting information, our perception alternates between the two interpretations rather than combining them into one percept.⁶ This phenomenon turned out to be an excellent tool for correlating neuronal activity with subjective experience. In a series of experiments, Logothetis and his collaborators (Logothetis & Schall 1989; Logothetis & Leopold 1996) presented monkeys with motions in different directions in each eye while recording from area MT (medial temporal cortex; believed to process primarily visual motion). Many neurons fired as a response to the retinal stimulus (i.e., they fired whenever their preferred direction of motion was presented to either eye, regardless of the perception of the monkey). However, the activity of other neurons reflected the reports of the monkey (i.e., fired to their preferred direction of motion only if it was presented to the "active" eye). These neurons are likely to reflect the subjective rather than sensory experience. Similar findings were obtained from cells in V4 (Leopold & Logothetis 1996), when the conflicting stimuli were gratings in different orientations. Because these neurons reside in the deeper layers of the cortex, this activity is likely to be projected to other areas. Tracking the destination of these projections has a good potential of revealing areas that are more closely involved in visual awareness (Koch & Braun 1996).

Subliminal visual priming — The basic phenomenon

Priming is often used as a tool for studying representations, but it can also be considered as a mediating phenomenon that allows the study of visual awareness during the different stages of object recognition. While recognizing

objects is often immediate and unambiguous, it is not clear at what stage do we become aware of the interpretation of the visual input. Studies addressing this and related questions will be reviewed here, as well as speculations regarding mechanisms and cortical localization.

In typical demonstrations of visual priming (Bartram 1974; Biederman & Cooper 1991; Schacter, Delaney & Merikle 1990), observers are generally able to name the stimulus on its first presentation. Priming is then manifested by improved performance in subsequent encounters with this stimulus (i.e., supraliminal priming). Can visual priming be evidenced even if the observer cannot recognize the prime, or even guess its name from among a few alternatives? As will become clearer in this section, priming of object recognition is possible although subjects are not aware of the identity of the prime, and a considerable amount of time and intervening information buffer between the prime and the test images.

In a study by Bar & Biederman (1998), line-drawing images of objects and animals were flashed very briefly (at an average of 48 ms), and were followed by a highly effective mask. Following each stimulus presentation, subjects were required to identify the object by name, even if they had to guess, and then to choose from four object names in a 4-alternative forced-choice (4AFC) test. The subsequent 4AFC task was used in order to assess the information extracted from unidentified presentations.⁷ The experiment included two blocks of pictures of objects. The objects in the second block had the same names as the objects in the first, and were presented in one of four possible conditions relative to the image with that name on block 1: either at the same or different position, and either with the same shape or as a different exemplar of the same object (Figure 1). Changes in position were incorporated to study translation invariance⁸ in subliminal priming, and to compare it with the complete translation invariance reported for supraliminal priming (Biederman & Cooper 1991). Different exemplars were used to assess a possible semantic component in the priming (Bartram 1974). (Stimulus-specific improvement can stem from either visual or semantic priming. Subtracting the priming of different-exemplar conditions from same-exemplar priming provide an assessment of visual and semantic priming.) Two control blocks were incorporated: one before the first experimental block, and the other after the second experimental block. The images of the second control block had different names than those in the first control block. Any improvement in naming objects in the second control block, compared with the first control

block, would represent general improvement that cannot be attributed to priming. Twenty images and fifteen minutes, on average, intervened between the first and second presentations of the same object.

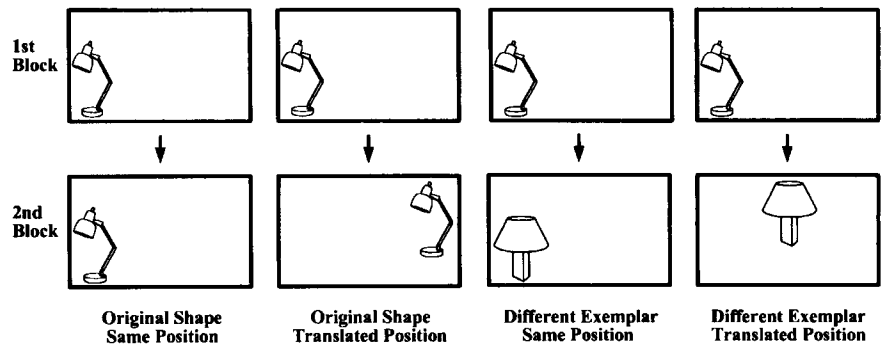


Figure 1: Each object from the first block repeated on the second block in one of four possible conditions. Shift in position was used to study translation invariance in subliminal priming, and different exemplars were used to estimate the semantic component in the priming.

Most of the experimental objects (86.5%) could not be identified on their first presentation (Figure 2). Accuracy increased substantially (21%) for naming objects of the same shape (i.e., same exemplars) when they repeated at the same location on the second block. The 4% increase in accuracy of naming the control objects over the course of the experiment reflects general improvement that is not attributable to priming. The 17% advantage of the same shape, same position objects over the second block control objects is therefore a manifestation of priming. When the same shape was repeated at a different position, the magnitude of priming was reduced to 8%. No priming was evident for the different exemplar conditions. Therefore, all the priming of the same-shape objects was visual; none could be attributed to verbal or semantic factors.⁹

Performance in the 4AFC test on the first block for objects that could not be named was at chance (25%). Consequently, we can assume that subjects were not aware of the identity of the objects that they could not name. Therefore, the priming was subliminal. This is the first demonstration of

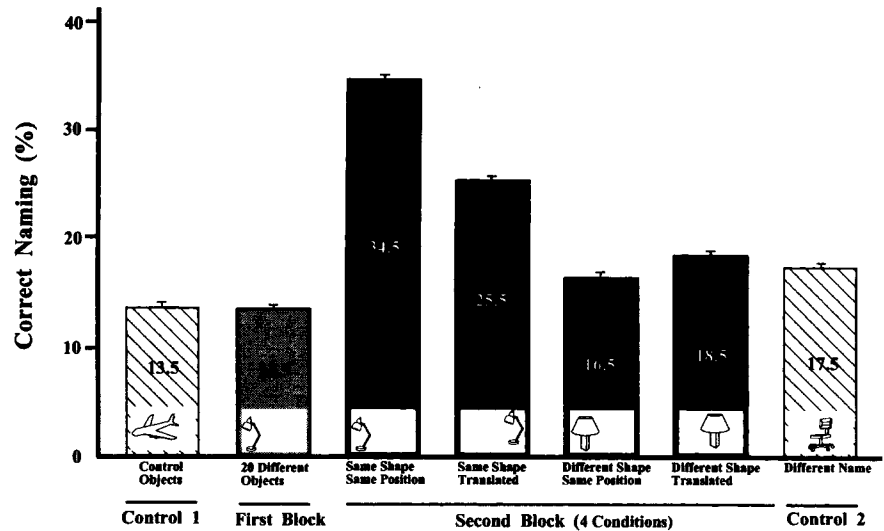


Figure 2: Percent correct in the naming task. Repeating the same image in the same position improved identification markedly. Translating the second presentation of the same image reduced but did not eliminate the priming. Objects with the same name but different shape (i.e., different exemplars) demonstrated no significant priming. (After Bar & Biederman 1998, with permission.)

facilitatory visual recognition priming by unidentified pictures when the subject could not anticipate if, when, or where the previously unidentified picture was to be shown again.

It is always possible to argue that subjects experienced a fleeting awareness (Crick & Koch 1990) during a subliminal presentation but could not report it. The *attentional blink* is one such example. In a rapid serial visual presentation (RSVP) of words, it has been demonstrated that subjects are "blind" to stimuli appearing during the first 400–600 ms following the target they have to detect (Shapiro, Raymond & Arnell 1994). For example, if the sequence of images includes A – B – F – G – H – K – J – Y – T (where different letters here represent different stimuli in the experiment), and subjects have to detect both H and K, the K would be detectable only if it is separated by more than 500 ms (on average) from the H. Using event-related potentials (ERP), it was later shown that subjects can, in fact, recognize the stimuli presented during the attentional blink (Luck, Vogel & Shapiro 1996),

but fail to report it. This result suggests that subjects were aware of the identity for some time but could not report it when asked. Further experiments are required in order to determine whether the backward masking used with the brief presentations of stimuli in the Bar & Biederman (1998) study interfered with processing or reporting.

Cortical regions mediating awareness of object identity

Little is known about the neural mechanisms underlying visual priming. Nevertheless, the studies reviewed above allow for several conjectures and speculations that will be described here, following a brief introduction on the functional organization of visual cortex.

From the primary visual cortex, V1, information is propagated along two main pathways: the ventral and the dorsal (Ungerleider & Mishkin 1982). The dorsal pathway processes information such as object position, size, and orientation, that is typically used for motor interactions. The ventral pathway, V1 → V2 → V4 → inferior temporal (IT), is believed to be responsible for the processing of shape and other cues of identity, and is largely invariant to transformations in position, size, and (to a certain extent) depth rotation. The anterior part of IT (area TE) is the last solely visual area. It is thus considered the "output" of the ventral visual pathway, and is the main source of projection to areas outside the visual cortex such as the hippocampus, prefrontal cortex, amygdala, and basal ganglia. Lesion studies suggest that while area IT serves short-term memory for shape, the projections to the hippocampus are vital for long-term coding (Miyashita 1993).

Neurons of the temporal visual cortex in the macaque are ordered in a rough hierarchy along two dimensions: cells in anterior areas have larger receptive fields (RFs), and they prefer more complex features than cells in posterior areas. Therefore, cells in the primary visual cortex (V1) have small RFs (typically $< 1^\circ$; Roe & Ts'o 1995), and are sensitive to simple stimuli (e.g., oriented lines). On the other hand, cells in IT are sensitive to complex stimuli (e.g., faces), and have large RFs (averaging 26° ; Desimone & Gross 1979). RFs in IT, however, vary largely within its subdivisions: RFs in its posterior part (area TEO) are similar to those of cells in V4 (Boussaoud, Desimone & Ungerleider 1991), whereas RFs in its anterior part, area TE, can be as large as 60° (Desimone & Gross 1979). Lesion studies in the subdivi-

sions of IT indicate that TEO is important for pattern discrimination while TE is vital for object memory (Iwai & Mishkin 1968; Iwai & Mishkin 1969). Furthermore, stimulus familiarization affects the tuning of IT cells (Ringo 1996), and object naming produces enhanced activation in that area (Martin, Wiggs, Ungerleider & Haxby 1996). Consequently, area IT is believed to have a fundamental role in visual object recognition (Kobatake & Tanaka 1994; Miyashita 1993).

In light of this cortical organization, Bar and Biederman (1998) proposed that one possible interpretation of their results is that the first presentations that were not identified did not affect a sufficient number of the cells representing that object in TE. Therefore, it is possible that the subliminal priming is a consequence of a change in intermediate areas prior to TE. These intermediate representations might not be available for conscious report such as naming, but, when combined with the activity of a second presentation of the same stimulus, the resultant activity might be sufficient for identification.

Bar and Biederman (1998) noted that this hypothesis is consistent with the size of RFs of cells in the ventral visual pathway, and the effect of translation on subliminal visual priming.¹⁰ Cells with larger RFs have a greater chance of being activated by translated presentations, and cells in different visual areas have RFs of different sizes. Therefore, priming that is mediated by different areas will result in different degrees of position invariance. For example, when most of the objects were recognizable also on the first block (i.e., supraliminal), priming has been shown to be completely translation invariant for a translation extent of 4.8° (Biederman & Cooper 1991). Supraliminal visual priming is therefore likely to affect an area with RFs large enough to accommodate such translation (e.g., TE).

The 4.9° shift that was used in the Bar & Biederman (1998) experiment cannot be accommodated at all by the small RFs of cells in early areas such as V1/V2, but would be fully accommodated by the large RFs of most cells in TE, resulting in a complete translation invariance. Therefore, we proposed that partial translation cost indicates that the effect of subliminal visual priming may be concentrated in a cortical area where cells have RFs of intermediate size. Likely candidates are the human homologues of areas V4, where the RFs size, 0.7° — 10° (Tanaka, Weber & Creutzfeldt 1986)¹¹ would straddle the 4.9° shift, and TEO in which cells have RFs similar to those of V4.

This hypothesis was later tested (Bar & Biederman 1999) by comparing the properties of subliminal visual priming with known physiological charac-

teristics of cells in intermediate visual areas. Namely, using the propensity of cells in V4 and TEO to have RFs that are confined to a single quadrant of the visual field (Boussaoud, Desimone, & Ungerleider 1991). Cells in area TE, on the other hand, have RFs that often cover multiple quadrants. In this experiment, images were translated either between different quadrants or within the same quadrant. Subliminal priming was obtained only for images that remained within the same quadrant in both prime and test trials. In other words, although the extent of translation and eccentricity were identical in both conditions, crossing a midline of the visual field eliminated the priming. Therefore, subliminal visual priming is likely mediated by cortical areas in which cells have RFs large enough to respond to both presentations of a stimulus shifted 4.8°, but at the same time are confined to a single quadrant (e.g., V4, and TEO). Consequently, visual awareness of object identity might be associated exclusively with activity at area TE or beyond.

A recent functional Magnetic Resonance Imaging (fMRI) study was designed to address the cortical mechanisms associated exclusively with conscious object recognition (Bar *et al.* 1999), using subliminal visual priming as a tool. The specific goal was to image the cortical activity elicited by trials in which participants were able to recognize pictures of familiar objects, and to compare it with the activity elicited by trials in which they could not recognize the same set of objects. The visual stimulation and the task requirements were identical in both cases; the only difference was subjects' ability to identify the objects. Consequently, any resulting differential activity should reveal the cortical focus and dynamics directly associated with the moment when subjects can first recognize an object explicitly.

Participants were scanned while they performed an object recognition task. In this task, pictures of familiar objects were presented very briefly, interposed between two masks. Participants were required to recognize each of the objects and to respond by pressing one of four buttons, indicating their level of confidence as to the identity of the object. The same object image was repeated, intermixed with the presentation of the other objects, for up to five times. As demonstrated by reports of subliminal visual priming (Bar & Biederman 1998, 1999), presenting the same objects repeatedly provides participants with multiple opportunities for successful recognition of those objects.

A visual cortical focus in the anterior fusiform gyrus was identified that was modulated exclusively by the ability to recognize objects. As subjects gained more information regarding an object's identity, activity in the tempo-

ral lobe intensified and propagated anteriorly and laterally. These findings support reports of single-unit studies in monkeys that revealed a cortical hierarchy of object representation in the temporal lobe. We suggested that information about objects is also represented in the fusiform in a hierarchical manner, such that shape properties and appearance-related information are represented in the posterior parts of the fusiform, whereas knowledge about object name and meaning is represented in the anterior parts.

Furthermore, these results suggest that the frontal cortex may have a special role in coping with difficult tasks such as recognition of briefly presented objects. Because the activity in the frontal lobe was more substantial in the masked presentations, it may reflect a general increased effort during the recognition attempt, or the manifestation of feedback signals and top-down processes, which may have had a more central role in the masked trials. This activation is possibly related to the semantic analysis involved in recognition. At the moment, it cannot be determined whether this frontal activity started only after recognition has been accomplished, or already before that moment. However, it is conceivable that when recognition is difficult (e.g., brief and masked presentations), top-down processes could facilitate successful recognition (Ullman 1995), and therefore may be expected to be active even before recognition has been accomplished.

Dissociation and cooperation in visual cognition

Priming in general, and subliminal visual priming in particular, can be seen as empirical support for the possibility that processes of which subjects are unaware can nevertheless facilitate performance. Before turning to describe more examples of facilitatory nonconscious contribution, two exceptions will be mentioned. The first is *negative priming*. In a typical study of negative priming (Tipper 1985; DeSchepper & Treisman 1996), two superimposed shapes, in different colors, are presented on each trial. Subjects are required to ignore one of them (e.g., the red) and attend the other (e.g., the green). If the stimuli are pictures of familiar objects, the task is often to name the attended object as fast as possible. If the stimuli are novel unfamiliar shapes, a typical task is a match-to-sample. The general finding is that when a previously ignored object becomes the relevant object in another trial (by switching its color to green), response time is significantly slower. Although the increase is

often modest (tens of ms), the effect has been found to be robust. Therefore, in negative priming, implicit knowledge from the priming stage interferes with subsequent performance without subjects' intention.

A second exception is the inclusion-exclusion dissociation task of Jacoby (1991). As reviewed earlier, Jacoby and his colleagues (Jacoby *et al.* 1993; Debnar & Jacoby 1994) found that subliminally presented words were given equally often in inclusion and exclusion tasks, suggesting a nonintentional use of memory. Both instances are taken to reflect involuntary processing that degrades, rather than facilitates performance.

In addition to visual priming of object recognition, in which subjects gain information of which they are not aware, there are other examples of sub-threshold stimuli that affect performance in a way that supports a "dissociation but cooperation" principle. Two studies that will be reviewed in this context represent two extremes: one involves cognitive judgments of liking, and the other includes low-level perceptual tasks such as orientation detection of basic spatial cues.

In the first study (Murphy & Zajonc 1993), non-Chinese speakers were required to rank their liking of Chinese ideographs. The ideographs were preceded by a prime stimulus: a face with either an angry or a happy expression. The primes were presented half of the time above threshold and half of the time subliminally (such that subjects could not even detect that there was a prime on those trials). The affective prime biased the judgment so that priming with a happy face resulted in an increased liking of the ideographs, and priming with an angry face resulted in a decreased liking of the ideographs. While the influence of subliminal priming on affective judgments has been demonstrated in the past (Zajonc 1968), it is interesting that in the study of Murphy & Zajonc the prime itself is a highly complex stimulus and is likely to be analyzed by cells in IT (Rolls & Tovee 1994). Therefore, durations that were too fast for detecting the presence of the prime were nevertheless sufficient for interpreting the face expression.

In another study (Tanaka & Sagi 1998), subjects had to detect oriented gratings (a Gabor signal in this case) that were presented for 90 ms, and that were preceded by a prime stimulus that had the same spatial frequency but a different contrast. The contrast of the prime could be either very low (near-threshold), or high enough to be detectable. Priming the target with a subliminal prime facilitated detection by 40%. This priming effect could persist for as long as 16 seconds. High contrast primes (supraliminal) did not facilitate the

detection of the target. Therefore, a sub-threshold stimulus may facilitate performance with targets of different complexity, and in various tasks.

Stimuli such as gratings are usually analyzed and resolved by earlier visual areas (e.g., V1/V2). On the other hand, subliminal visual priming in object recognition has been suggested by Bar and Biederman (1998; 1999) to take place higher along the ventral pathway (e.g., V4 or TEO), whereas supraliminal priming is likely to affect even higher areas such as TE. In spite of the different loci, these different types of priming all seem to manifest similar cooperation between nonconscious gain and subsequent explicit reports.

Correlating visual awareness with cortical activity

If we could measure all the activity elicited by a brief presentation, and could define the visual properties to which this activity corresponds, then we could compare it with subjects' report. Any difference is likely to represent activity, and possibly knowledge, of which subjects were not aware. For example, if we know that a certain stimulus elicited activity in an (imaginary) area that is dedicated to, say, "circles-processing," and at the same time the subject cannot report seeing circles, we can say that the subject is unaware of the activity in that area. Using picture naming and 4AFC tests provided one end of this contrast: an assessment of subjective awareness of object identity. A comparison will now be made between this behavioral assessment and physiological data obtained in similar experimental designs.

In an imaging study of the cortical activity during object classification, subjects had to judge if there was an animal in a briefly presented picture (Thorpe, Fize & Marlot 1996). The stimuli were color photographs of natural scenes that were presented for 20 ms. An ERP signal in the frontal cortex was found to be discriminative even for such brief exposure durations. Therefore, 20 ms presentations were sufficient for processing the visual information required for performing this detection task. However, the images in this study were not masked. It might be that the same discriminative activity would not develop when a mask follows the stimuli.

In another study (Rolls & Tovee 1994), pictures of faces were presented for 16 ms, and were either followed by a mask or not. Activity of single cells in the visual temporal cortex of macaques (superior temporal sulcus; STS) was

recorded while the animals viewed these brief presentations. When there was no mask, the response of the cells lasted for 200–300 ms, perhaps to allow memory consolidation (Potter 1976; Biederman, Subramaniam & Madigan 1994). However, this prolonged activity was reduced by masking, such that cells fired for 20–30 ms before the mask interrupted their activity. Analysis using techniques from information theory (Tovee, Rolls, Treves & Bellis 1993) suggested that the first 20 ms of activity contained 64.9% of the information available from the total prolonged response of the cell, and 50 ms contained 87%.¹² Therefore, (a) masked presentations in the range of 20–40 ms can be sufficient for performing high-level visual tasks (though it is not clear that these durations would suffice for more complicated tasks such as object naming), (b) the response of cells in IT to a brief stimulus is sustained for much longer than is required for certain discrimination tasks, and (c) this response is gradually more diagnostic of the object.

The stimuli in those experiments were faces, rather than objects. Faces differ from other objects in many respects (e.g., frequency of occurrence, social and ecological importance, and class-similarity), and they thus might have different cortical substrates and underlying mechanisms. The next study that will be described in this context, then, is a study where the stimuli were masked line drawings, and thus more similar to the stimuli of Bar and Biederman (1998).

In studying the cortical correlates of visual masking in IT, Kovács, Vogels, and Orban (1995) demonstrated that the mask does not reduce the response of cells in TEO and TE to the target, but rather shortens it. Before the effect of the mask, the activity during the first 20 ms was shape-specific. In addition, the average number of spikes in the first 20 ms period of the response was not significantly different in the masked and unmasked conditions. However, when a mask did not follow the 20 ms presentation, the shape-selective response persisted much longer. Therefore, these results extend those of Rolls and his colleagues to masked line drawings.

It seems that during the initial response the cells “know” more than the monkey can report. One possible, though speculative, account is the following: Assume that it takes cells in area TE (or an area to which TE is projecting) some time to reach the “final decision” as to the identity of the stimulus, such that eventually only the population that represents the specific object continues to fire. This interval is likely to stem from a need for integration of incoming information over time, for binding complex features, or for selecting

the correct identity from among multiple possible interpretations of the input, and is often very short. Indeed, recent physiological evidence (Tamura & Tanaka 1997) suggests that the response of cells in the visual cortex to an image of an object is initially broad and less selective, and gradually reduces while becoming more stimulus-specific.

A similar fine-tuning process is assumed to take place in all areas of the visual ventral pathway such that each area processes over time the information that is projected to it from other areas, and gradually (though within a short interval) projects information that is more and more accurate. We may consider the initial, coarse activity as a set of multiple hypotheses regarding the identity (see also Ullman 1995). For example, if the initial (possibly crude) information will be first interpreted as a "circle," the cells that represent a ball, a coin, and a plate will all be active because they all have the "circular" property. As the incoming information is becoming more accurate (or fine-tuned), only one representation will remain active, the one that best corresponds to the specific object, while the others will be suppressed.

Projecting these results, analysis, and proposal to the findings of Bar & Biederman (1998), it seems that the brief presentation durations are capable of activating cells probably even in TE. This activity might have contained sufficient information to specify the identity of the object. The reason subjects could not report the stimulus might be that they were not aware of this activity as it was not sufficiently "fine-tuned," and that the mask interfered before the fine-tuning has been completed (Bar, submitted).

Summary

In the studies reviewed here, performance was often improved in spite of the dissociation between the implicit gain and explicit reports. The phenomenon of subliminal visual priming was reviewed here as an instance of such nonconscious interaction that promotes conscious knowledge.

The effect of a primed image, even if it is unidentified, is robust over time and intervening information. It is therefore likely to be accompanied by long lasting synaptic modifications. A hypothesis as to the cortical localization of subliminal visual priming suggests that the locus of this interaction be in an intermediate site along the visual cortex (Bar & Biederman 1998; 1999). Nevertheless, priming demonstrated in different tasks might affect different

cortical areas, and therefore such interaction might take place in several possible loci along the visual cortex. The level at which subjects are aware of the prime stimulus likely depends on the area in which priming has concentrated. Consequently, the information subjects can report explicitly is determined by the complexity of the visual information that is processed by the primed area.

In addition, it was also suggested that observers become aware of certain visual aspects of the input only after their analysis have been accomplished to a certain degree. This can be achieved via a gating mechanism that projects information to areas such as the prefrontal cortex only after the sensory information has been fine-tuned sufficiently to allow an unequivocal interpretation of the input. Such gating mechanism should exist in conjunction with other mechanisms that permit quick and coarse analysis of the input to facilitate processes that aid survival (e.g., fight-or-flight).

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Notes

1. In word stem completion tests, the task is usually to complete a stem with the first word that comes to mind. This test might be preceded by a study phase in which subjects are presented with a list of words.
2. Object *naming*, *identification*, and *recognition* are all considered equivalent here. In all three, subjects have to recognize the identity of an object by providing its name.
3. The discussion here is limited to visual awareness, which is narrower than self-awareness.
4. In the divided attention condition, subjects were also required to add two digits that flank the study word.
5. Baseline performance was defined as the frequency of providing a word from the study list as a completion in a non-match trial.
6. The conflicting information is initially fused, and the alterations begin only after a few seconds.

7. In one of the most comprehensive critiques of subliminal (semantic) perception, Holender (1986) asserted that forced-choice tests are exclusive measures of awareness. Tasks such as forced-choice are optimal as they rule out effects of intention, and by this are likely to "filter" the subjective component of the response.
8. Translation invariance is the invariance in the magnitude of priming to changes in position between prime and test presentations.
9. The subjective impression, occasionally volunteered by the participants, was that the primed images (those that were recognized correctly only on the second block) were presented for a longer duration. Interestingly, Witherspoon & Allan (1985) have found that when subjects had to judge temporal durations of briefly presented words, they tended to overestimate the duration of words that were presented before, compared with their judgment of novel words.
10. It is assumed that priming requires reactivation of the same cells that were initially activated by the prime. Consequently, translation invariance is obtained when the new stimulus position allows activation of the previously activated cells.
11. Assuming that the size of RFs of humans are similar to those of monkeys.
12. In this regard, it is interesting that it is difficult to associate the 87% knowledge contained in the first 50 ms of activity reported by Tovee *et al.* (1993) with subjects' performance. For example, does 87% include figural detail? Global shape? Aspect-ratio? Being able to name the object might require exactly 100%.

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