Recognizing Threat: A Simple Geometric Shape Activates Neural Circuitry for Threat Detection

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Abstract

■ The urgent need to recognize danger quickly has been shown to rely on preferential processing in dedicated neural circuitry. In previous behavioral studies examining the pattern of the face when displaying anger, we found evidence that simple noncontextual geometric shapes containing downward-pointing V-shaped angles activate the perception of threat. We here report that the neural circuitry known to be mobilized by many realistic, contextual threatening displays is also triggered by the simplest form of this V-shaped movement pattern, a downward-pointing triangle. Specifically, we show that simple geometric forms containing only downward-pointing V-shapes elicit greater activation of the amygdala, subgenual anterior cingulate cortex, superior temporal gyrus, and fusiform gyrus, as well as extrastriate visual regions, than do presentations of the identical V-shape pointing upward. Thus, this simple V-shape is capable of activating neural networks instantiating detection of threat and negative affect, suggesting that recognition of potential danger may be based, in part, on very simple, context-free visual cues. ■

INTRODUCTION

The successful regulation of human interaction rests on the accurate comprehension of the intentions of others. This basic requirement led Darwin (1872/1998) to suggest that human facial displays of emotion provided a reliable communication system that used a common biological foundation to express and comprehend meanings in similar ways across all cultures. In order to determine key stimuli that convey these semantic meanings, and the mechanisms associated with their recognition, the research reported here used functional magnetic resonance imaging (fMRI) to determine whether a configurational pattern initially associated with threatening facial expressions, but stripped of all contextual meaning, leaving only a simple geometric shape, is sufficient to trigger specific emotion-related neural circuitry that previously has been shown to respond to threat-related stimuli.

Darwin's proposal regarding universal signals contained in emotional expressions found support in major programs of research directed by Ekman (1973, 2003) and others that identified the global expressions characteristic of each emotion as well as the exact movements (Ekman, Friesen, & Hager, 2002) of the facial muscles through which these displays are formed. Ekman (2003) also suggested that these displays are identified by sets of feature detectors that permit the rapid recognition of a facial expression. Although Ekman reviewed evidence clarifying the expressions associated with each emotion, how an emotion is recognized is understood much less well. Given the evolutionary advantage of rapid detection of threat (Lundqvist & Öhman, 2005; Hansen & Hansen, 1988), we focused on the mechanisms underlying the recognition of facial expressions of anger. As these investigators have maintained, because of the survival advantage conferred by early recognition of potential danger, this process likely relies on neural circuitry that triggers rapidly, relatively automatically, and with minimal sensory input (Öhman & Mineka, 2001; LeDoux, 2000). Further, as rapid detection is facilitated when visual signals of threat share easily identifiable features, thus reducing the need for thorough processing of all the features that compose a threatening stimulus, it would be highly efficient if such appraisal systems were organized to respond to an overall visual configuration formed by the facial features, rather than require the inspection of each movement of each facial landmark. As Ekman's proposed feature detectors are thought to be associated with dedicated neural circuitry activated by the visual configurations formed when expressing an emotion, this study focuses on identifying the most essential underlying visual cues need to express threat-related emotion.

The behavioral basis for this hypothesis rests on studies that used multiple methods to isolate key stimuli that convey affective meaning. Seeking to identify the specific sign stimuli that conveyed the meaning of anger and happiness across a wide range of primarily nonliterate tribal cultures, cross-cultural research (Aronoff, Barclay, & Stevenson, 1988) found that the affective

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identity of the display was carried in the overall configuration made by the major landmarks of the face, rather than by the specific facial features themselves. Anger was shown to be conveyed by angular and diagonal forms made by the facial features (e.g., eyebrows), especially acute angles pointing downward, and happiness was conveyed by curved patterns. This configurational hypothesis is also supported by Bassili's (1978) pioneering point-light experiment, which studied the overall geometric pattern formed by the movement of the face as a whole when displaying an emotional expression. Bassili placed luminescent dots on subjects' faces and, in a dark room, asked them to assume happy and angry expressions. When portraying a happy appearance, the burst of dots expanded outward to form a rounded shape, whereas in the angry representation, the points of light imploded downward and inward to form a V-shaped figure. The ability of the V-shaped figure (usually representing eyebrows) to convey an angry subjective state is also shown in the many studies using schematic faces (Lundqvist, Esteves, & Öhman, 1999) and confirmed by studies (Lundqvist, Esteves, & Öhman, 2004) which show that V-shaped figures elicit this emotional meaning even when presented without any other facial feature. The power of more rounded facial shapes to convey emotionally positive semantic meanings (Zebrowitz, 1998; Hildebrandt & Fitzgerald, 1983) is similarly well established.

These initial findings have been confirmed by additional naturalistic and experimental research (Aronoff, Woike, & Hyman, 1992; Aronoff et al., 1988), which examined the affective identity of a wide range of nonrepresentational visual stimuli, such as angular or curved lines, as well as similar geometric shapes using figures far removed from actual representations of the human face. Abstract shapes and everyday objects (e.g., watch, sofa) containing sharp angles of various orientations have also been found to be less preferred than the similar shapes or objects containing curved forms (Bar & Neta, 2006). Bar and Neta (2006) posited that the lower preference for sharp innocuous objects ''stemmed from a feeling of threat, and that this feeling was triggered by the sharpness of the angles per se'' (p. 647). Other work in our laboratory attempted to identify the key features underlying facial cues of emotion by gradually stripping away contextual information and reducing the stimuli to their most fundamental geometric components. In several studies using semantic differential scales (Osgood, Suci, & Tannenbaum, 1957) to record the subjective meaning elicited by these nonrepresentational visual stimuli (i.e., the degree of ''badness,'' ''potency,'' and ''activity'' perceived in the stimuli), and following techniques introduced by Tinbergen (Eibl-Eibesfeldt, 1989), who pioneered the use of models to study signaling devices, we presented increasingly angular, diagonal, or curvilinear models for examination and found that angular V-shaped figures alone (similar to the angles found in the eyebrows, cheeks, chin, and jaws in angry expressions) and rounded figures alone (similar to the curves found in the cheeks, eyes, and mouth in happy expressions) conveyed the same affective meanings as that evoked by actual angry and happy facial representations (Aronoff, 2006; Aronoff et al., 1988, 1992). Using the same technique, we recently extended this finding, reporting that simple geometric shapes are perceived as having affective value, and furthermore, that the orientation of the angle is an important determinant of this value. Specifically, simple shapes containing a downward-pointing acute angle (e.g., a ''V,'' a triangle) were rated by participants as more threatening than the exact same shapes with the V-angle pointing upward (Larson, Aronoff, & Stearns, 2007).

Additional support for the configurational hypothesis is provided by the many studies which examine the efficiency of shapes to signal potential threat. Resting again on Darwin's suggestion that speedy detection of threat confers an evolutionary advantage (Niedenthal & Kitayama, 1994), Hansen and Hansen (1988) used the visual search paradigm to show that the search for an angry face in a crowd of happy faces is more efficient (i.e., rapid) than the reverse. Subsequent work of this type, using both real and schematic faces (Horstmann & Bauland, 2006; Öhman, Lundqvist, & Esteves, 2001), confirmed that angry faces consistently lead to briefer search times. In an experiment to isolate capture of attention effects for the pure geometrical form of a downward-pointing acute angle from other facial features and from other confounding perceptual factors, we used a simple triangle whose vertex was pointed either up or down as our target shape (Larson et al., 2007). Triangles were used rather than a ''V'' itself to avoid the possibility that capture of attention was facilitated because V is a letter, rather than due to any inherent emotional or attentional properties. Thus, having a simple shape that varied only in the orientation of the acute angle, we demonstrated that a triangle with a downward-pointing vertex is recognized more rapidly than the identical shape with an upward-pointing vertex. Further, this study also provided evidence that the downward-pointing triangle has the power to elicit sustained attention, in keeping with the ability of realistic threat-related stimuli to disrupt or slow performance of ongoing cognitive tasks (Eastwood, Smilek, & Merikle, 2003; Vuilleumier, Armony, Driver, & Dolan, 2001; White, 1995).

Thus, both subjectively and attentionally, the simple downward V-shape appears to function much like a typical contextually based threat stimulus. These results lead us to hypothesize the presence of a neural network of targeted, and thus, highly efficient brain regions that can identify molar shapes that signal the presence of biologically relevant affective stimuli. Such configurational detection mechanisms seem to be a much more parsimonious way to account for the decoding of emotional displays than would be the conjecture of a wide set of specialized neural circuitry isomorphic with each individual muscular movement. Thus, the evolutionary advantage for threat detection may be due, in part, to facilitated recognition of a simple geometric form, common to a number of threat-related objects, thereby minimizing the need to process a stimulus fully and in context in order to identify a potential threat. For these reasons, in the present study, we investigate whether viewing the simple shape of a downward-pointing acute angle recruits the same neural circuitry as that demonstrated previously to respond to representational and contextual cues of threat, such as threat-related facial expressions, aversive scenes, and phobogenic stimuli.

A large body of research has implicated the amygdala in directing attention toward biologically relevant, affectively salient information, as well as in the processing of aversive stimuli (LeDoux, 2000); functions that render the amygdala particularly important in the detection of potential threat. Human neuroimaging studies have demonstrated increased amygdala activation in response to a number of aversive stimuli, including negatively valenced pictures (Irwin et al., 1996), angry faces (Kesler-West et al., 2001), and fear faces (Vuilleumier, Armony, Driver, & Dolan, 2003; Morris et al., 1998). Other work has further supported the notion that the amygdala instantiates rapid, automatic detection of threat, even under conditions in which attention is limited (Anderson & Phelps, 2001) or directed away from threat-related stimuli (Vuilleumier et al., 2001). Human amygdala activation has also been detected in response to coarse, spatially degraded facial cues of threat (Vuilleumier et al., 2003). Importantly, evidence from fear conditioning studies in animals demonstrates that an intact amygdala is sufficient for rats to learn to fear very simple stimuli (e.g., simple tones) even when input from higher cortical regions is disrupted through lesions of the relevant modality-specific sensory cortex (Doron & LeDoux, 1999). Of particular relevance for the present study, Bar and Neta (2007) found that neutral objects (abstract figures, everyday objects) containing sharp as compared to curved contours activated the amygdala, among other regions. Similar to the principles guiding the present work, the authors interpreted these findings as further support for the notion that sharp, angular objects may signal danger.

In light of recent evidence, we also expected to see activation in visual sensory pathways in response to the downward V-shape. In a recent review, Vuilleumier and Driver (2007) emphasized that affective, not just perceptual, properties of visual stimuli can be potent modulators of the visual cortex. Consistent with this premise, emotional, particularly unpleasant emotional, faces activate the face-sensitive region of the fusiform gyrus more strongly than neutral faces (Vuilleumier et al., 2001). Similarly, unpleasant scenes elicit more robust activation of the extrastriate cortex than neutral scenes (Sabatinelli, Lang, Keil, & Bradley, 2007). This enhanced sensory processing is likely a function of the heightened salience of these stimuli, which necessitates increased recruitment of attentional resources, including the sensory cortex. The amygdala has been shown to be crucial to facilitate this enhanced processing in the ventral visual pathway (Vuilleumier, Richardson, Armony, Driver, & Dolan, 2004), and thus, seems to be the key structure initiating preferential processing of salient, biologically relevant visual stimuli.

We sought to determine whether the amygdala and related circuitry is recruited in response to a very simple geometric shape which is devoid of contextual affective cues, but has been shown to depict threat. Specifically, we predicted that shapes with downward-pointing V's would elicit greater amygdala activation than the identical shape whose vertex pointed upward. Consistent with the work of Vuilleumier and Driver (2007), we also predicted greater activation in ventral visual processing regions, as well as increased connectivity between the amygdala and these areas. Whole-brain fMRI scans were conducted while participants viewed a large set of images of three simple geometric shapes: downward-pointing triangles, upward-pointing triangles, and circles that varied in number, size, and location (see Figure 1) in a block design. To maintain attention, participants made simple judgments about the number of shapes depicted in each image. As with our previous behavioral work, triangles were used rather than an open V to avoid the possible

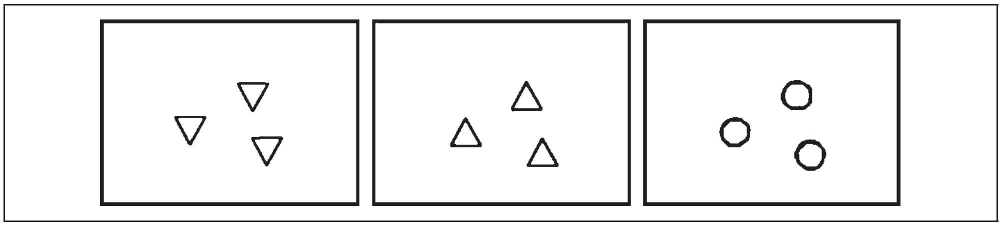

Figure 1. fMRI paradigm and examples of shape stimuli. Across four runs, 12 blocks of each of the three stimulus types, downward-pointing triangles, upward-pointing triangles, and circles, were presented in a random order. Each block was 25 sec long and consisted of 10 different stimuli of the same shape, each presented for 2.5 sec. Each stimulus consisted of one to seven identical shapes. Shapes of four different sizes were presented, but size was held constant within any given image. The number, size, and location of the shapes were counterbalanced within a condition and were equated across the three different shape conditions. To ensure that participants maintained attention to the stimulus presentation, they were asked to press a button indicating whether greater or fewer than four shapes were presented in each image (no images contained four shapes). Each block was followed by a 15-sec rest period during which a fixation cross was displayed.

confound of V being a letter, and thus, being more salient. Upward-pointing triangles were used as a comparison condition in order to test the effects of the same shape when inverted. Circles provided another control condition and were selected to test the general effects of angular compared to nonangular stimuli.

METHODS

Participants

Twenty right-handed, healthy college students participated in this study and signed consent forms approved by the Michigan State University Institutional Review Board. Data from three subjects were discarded, one due to incorrect positioning of the equipment, another due to irregular anatomy, and a third due to lack of activation in primary visual areas suggesting lack of attention during the study. For the same reason, data from two functional runs were discarded in one of the remaining subjects, and data from one functional run were discarded in another subject. Seventeen subjects (10 men, mean age = 20.6 years, range = 18–26 years) were included in the data analysis.

Stimuli

Stimuli included 120 unique pictures for each of the three conditions: circles, upward triangles, and downward triangles (Figure 1). Each of the 120 pictures per condition was unique in either number of objects, object size, or object positions. Each picture contained one, two, three, five, six, or seven outlines of each shape on a white background. Shapes were presented in four different sizes, but for each picture the size was held constant. Finally, the positions were randomized within condition across all 120 images. Stimuli were matched across conditions such that, for each shape condition, there was an image that exactly matched the other conditions on number of objects, object size, and object position. Stimuli were displayed in color on a 640 × 480 LCD monitor mounted on top of the RF head coil. The LCD subtended 12° × 16° of visual angle.

Procedure

A block-design paradigm was controlled by an IFIS-SA system (Invivo, Gainesville, FL). Two ergonomic keypads were placed under the hands of each subject. The subject was requested to press the right index finger button when there were more than four objects on a picture, and to press the left index finger button when there were less than four objects (no image contained exactly four objects). Accuracy for this judgment was 99.7% and there were no reaction time differences between the three shape conditions.[1] Before entering the scanner, all subjects were trained by viewing a 2-min practice paradigm so that they became familiar with the task, and they were asked to pay close attention to the shape of the objects in each picture. Participants were told that the study aimed to understand how the visual system responds to different geometric shapes. The experiment was divided into four functional runs each lasting 6 min 15 sec. In each run, subjects were presented nine blocks of visual stimulation after an initial 15-sec ''resting'' period. In each block, 10 unique pictures from one condition were presented. Within a block, each picture was presented for 2.5 sec with no interstimulus interval. A 15-sec baseline condition (a white screen with a black fixation cross at the center) followed each block. Each condition was shown in three blocks per run. Both the order of conditions within each run and the order of pictures within a block were randomly determined. The four functional runs were presented to eight subjects in a forward order and others in a reverse order.

Image Acquisition

Data were collected on a 3-T GE Signa EXCITE scanner (GE Healthcare, Milwaukee, WI) with an eight-channel head coil. During each session, images were first acquired for the purpose of localization, followed by first and higher-order shimming procedures to improve magnetic field homogeneity (Kim, Adalsteinsson, Glover, & Spielman, 2002). To study brain function, echo-planar images, starting from the most inferior regions of the brain, were then acquired with the following parameters: 34 contiguous 3-mm axial slices in an interleaved order, TE = 27.7 msec, TR = 2500 msec, flip angle = 80°, FOV = 22 cm, matrix size = 64 × 64, ramp sampling, and with the first four data points discarded. Each volume of slices was acquired 146 times during each of the four functional runs while subjects viewed the pictures, resulting in a total of 584 volumes of images over the course of the entire experiment. After functional data acquisition, high-resolution volumetric T1-weighted spoiled gradient-recalled images with cerebrospinal fluid suppressed were obtained to cover the whole brain with one hundred twenty 1.5-mm sagittal slices, 8° flip angle, and 24 cm FOV. These images were used to identify anatomical locations.

fMRI Data Preprocessing and Analysis

All fMRI data preprocessing and analysis was conducted with AFNI software (Cox, 1996). For each subject, acquisition timing difference was first corrected for different slice locations. With the first functional image as the reference, rigid-body motion correction was done in three translational and three rotational directions. The amount of motion in these directions was estimated and then the estimations were used in data analysis. For each subject, spatial blurring with a full width half maximum of 4 mm was applied to reduce random noise (Parrish, Gitelman, LaBar, & Mesulam, 2000), and also to reduce the issue of intersubject anatomical variation and Talairach transformation variation during group analysis. For the group analysis, all images were converted to Talairach and Tournoux (1988) coordinate space with an interpolation to 1 mm^3 voxels.

For analysis of each individual subject, the reference function throughout all functional runs for each picture category was generated on the basis of the convolution of the stimulus input and a gamma function, modeled as the impulse response when each picture was presented. The acquired functional data were compared with the reference functions using the 3dDeconvolve software for multiple linear regression analysis and general linear tests (Ward, 2002). Multiple linear regressions were applied on a voxelwise basis for *t*-statistic tests and to find the magnitude change when each picture condition was presented, compared to the reference functions. BOLD percent signal change relative to the baseline state was then calculated. General linear tests were also applied on a voxelwise basis to find the statistical significance of pairwise comparisons for all the picture conditions. For the above analysis, in addition to applying the reference functions for the three picture conditions, MRI signal modeling also included the subject motion estimations in the three translational and the three rotational directions, and the constant, linear, and quadratic trends for each of the four functional runs.

Monte Carlo simulation of the effect of matrix and voxel sizes of the imaging volume, spatial correlation of voxels, voxel intensity thresholding, masking, and cluster identification was applied to estimate overall statistical significance with respect to the whole brain (Ward, 2000). Because the anterior cingulate cortex (ACC) was a specific region of interest (ROI), a similar procedure was carried to estimate the overall statistical significance with respect to this ROI.

Whole-brain Group Analysis

After the percent signal change was estimated with respect to each picture condition for each subject, an ANOVA was performed for group analysis with a mixed-effect two-factor model, with picture condition (three levels) modeled as a fixed effect and subject modeled as the second factor as a random effect. The ANOVA results were used to extract the activated voxels for all pairwise condition contrasts (voxel-based p value $<.005$ and whole-brain corrected p value $<.023$). The active voxel selection criteria required that the voxels were nearest-neighbor and within a cluster size of 248 mm^3. Based on application of these criteria to the whole brain (the medium size of the seventeen brains), the voxel-based p value $<5 \times 10^{-3}$ was corrected to be an equivalent of whole-brain corrected p value $<.023$.

Given the importance of the ACC in emotion and attention, we were also interested in activation in this region, particularly the subgenual ACC. As no cluster in this region met the aforementioned threshold criteria, we used the same Monte Carlo procedure to determine cluster size threshold using the ACC as the volume of interest rather than the whole brain. The combined right and left ACC with the medium size of all 17 subjects was used for this Monte Carlo simulation. It included 413 voxels at the resolution of echo-planar images, equivalently 14,662 mm^3. The ANOVA results were then used to extract the activated voxels for all pairwise condition contrasts in the ACC (voxel-based p value $<5 \times 10^{-3}$ and ROI corrected p value $<.026$). The active voxel selection criteria required that the voxels were nearest-neighbor and within a cluster size of 106 mm^3. Based on application of these criteria to the whole ACC (the medium size based on the 17 subjects), the voxel-based p value $<5 \times 10^{-3}$ was corrected to be an equivalent of ROI corrected p value $<.026$.

Functional Connectivity Analysis

To assess increases in coupling between the amygdala and other brain regions associated with threat, psychophysiological interaction analyses were conducted (Friston et al., 1997) using the amygdala cluster showing greater activation to downward compared to upward triangles as the seed region. A voxel-based multiple regression model including two first-order (main effect) terms and the interaction of the two was computed. The key term for determining increased coupling is the second-order interaction term involving BOLD fMRI signal extracted from a seed region, in this case, a 10-mm spherical ROI centered on the peak amygdala voxel for the contrast between downward- and upward-pointing triangles. The two first-order terms included: (1) a psychological variable, in this case, a modeled epoch for the downward- or the upward-pointing triangles convolved with a canonical hemodynamic response; and (2) the BOLD fMRI signal extracted from the amygdala seed region. Note that both the physiological and psychological variables were entered into the multiple regression analyses; in this way, results cannot be explained by the main effects of either, but only by the interaction. Resultant interaction beta weights from the downward- and upward-pointing triangle voxel-based multiple regressions were compared to one another using a paired *t* test. The *t* test results were used to extract the activated voxels (voxel-based p value $<5 \times 10^{-3}$ and whole-brain corrected p value $<.023$). The active voxel selection criteria required that the voxels were nearest-neighbor and within a cluster size of 248 mm^3. Based on application of these criteria to the whole brain (medium size of the 17 brains), the voxel-based p value $<.005^{-3}$ was corrected to be an equivalent of whole-brain corrected p value $<.023$.

RESULTS

Whole-brain Analysis: Brain Regions Activated by Viewing of Simple Shapes

Downward- Compared to Upward-pointing Triangles

Voxelwise group analyses revealed a greater BOLD response in the amygdala for downward- compared to upward-pointing triangles ($t = 3.63$, $p = .0002$, [−18, −4, −10], Figure 2A; Table 1; all t values, coordinates, and p values in text are reported for peak t value for that region). As the two conditions in this contrast involve presentation of the identical shape, this contrast illustrates that not only is the amygdala activated by a simple geometric shape but also that the orientation of the V angle is crucial for this activation. In addition to the amygdala, examination of other brain regions known to react to emotionally significant and threatening stimuli showed that there were significant BOLD responses for the downward minus upward triangle contrast in the subgenual ACC (Figure 2B; $t = 4.61$, [−9, 27, −7]), the left insula ($t = 3.82$, [−41, −28, 16]), and the bilateral superior temporal gyrus [STG] (L: $t = 3.80$, [−41, −30, 16]; R: $t = 3.82$, [56, −57, 14]). Greater activation for downward- compared to upward-pointing triangles was also observed in a region of the right fusiform gyrus that is somewhat anterior to, but, given the cluster size and extent, likely overlapping with the typically observed "fusiform face area" (Kanwisher, McDermott, & Chun, 1997; $t = 5.15$, [39, −41, −16]; Figure 2C).

In addition to these regions previously implicated in processing of affective stimuli, additional regions of the ventral visual pathway, as well as parietal visual attention areas, were also engaged in response to downward-pointing triangles (see Table 1). This includes the fusiform region mentioned above, as well as portions of the lingual and parahippocampal gyri in Brodmann's area 19, and the cuneus and the precuneus. A full list of the regions activated in response to downward- but not upward-pointing triangles is presented in Table 1.

No significant clusters were found indicating greater activation for upward- compared to downward-pointing triangles, suggesting that, in general, the brain preferentially processes downward acute angles.

Downward-pointing Triangles Compared to Circles

Interestingly, none of the predominantly affect perception-related regions listed above or in Table 1 were more strongly activated during viewing of downward-pointing triangles than circles in the whole-brain voxelwise analysis, nor was the face-sensitive region of the fusiform gyrus (see Table 1). The only regions demonstrating greater activation to downward-pointing triangles were areas of the ventral visual stream including the parahippocampal and lingual gyri, which were also identified in the contrast with upward-pointing triangles. However, as detailed in Table 1, the spatial extent of these areas of activation was, in general, much smaller for the comparison with

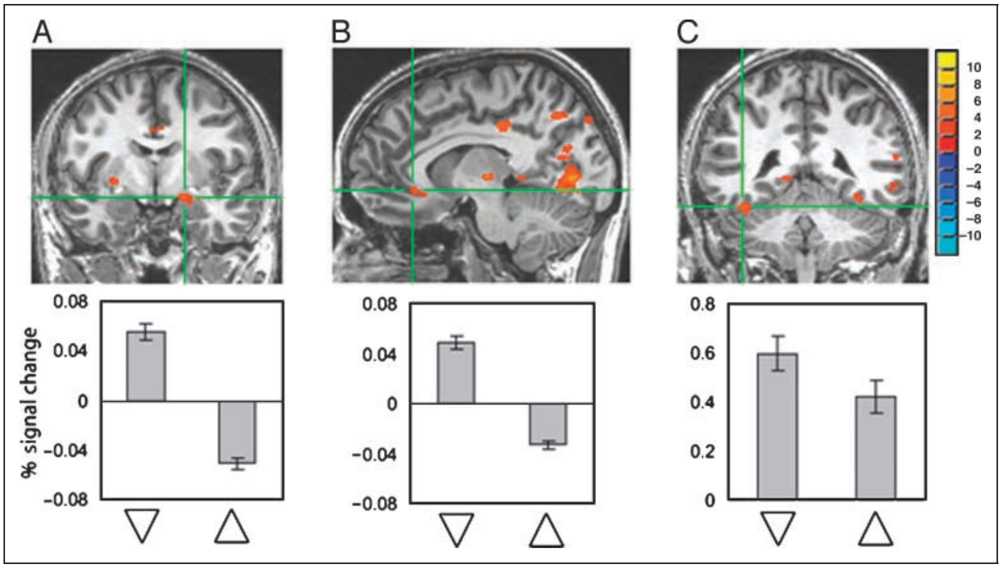

Figure 2. Illustration of greater activation for downward triangle minus upward triangle contrast in the (A) amygdala, (B) subgenual ACC, and (C) fusiform gyrus. A t statistic comparing percent signal change for each voxel was calculated and is plotted on the images in the top row. Mean percent signal change for the cluster is plotted in the bar graphs. Clusters of 248 mm^3 with a voxel-based p threshold of <.005 (a whole-brain corrected p threshold of .023) were considered statistically significant for (A) and (C). For the ACC, full ACC volume-specific criteria for clustering and statistical significance were applied requiring a cluster exceeding 106 mm^3 with a voxel-based p threshold of <.005 (a volume-corrected p of .026). The color scale to the left of the brain images represents the t statistic. Orange and red tones indicate greater percent signal change for downward compared to upward triangles. For panels A and C, images are presented in radiological convention, such that the right side of the image represents the left hemisphere. Greater activation for downward triangles was observed for all three regions. Maximum t value for each cluster and the Talairach coordinates of this value are as follows: left amygdala: $t = 3.63$, [−18, −4, −10]; right subgenual ACC: $t = 4.61$, [9, 29, −6]; right fusiform gyrus: $t = 5.15$, [39, −41, −16]. In each figure, the crosshairs are centered on the coordinates of the peak t value for the downward–upward triangle comparison. The coordinates of the fusiform gyrus activation overlap with the boundaries of the previously defined fusiform face area. Although other regions also showed greater activation for this contrast, the focus of the present article is on regions primarily implicated in affective processing.

Table 1. Regions Activated by Simple Geometric Shapes

		Downward Triangle > Upward Triangle			*Downward Triangle > Circle*			*Circle > Upward Triangle*		
Region		*Mean t Statistic*	*Volume (mm^3)*	*Coordinates x, y, z*	*Mean t Statistic*	*Volume (mm^3)*	*Coordinates x, y, z*	*Mean t Statistic*	*Volume (mm^3)*	*Coordinates x, y, z*
Predominantly Affect and Affect-perception Related Regions										
Amygdala	L	3.62	151	−18, −4, −10						
Insula	L	3.82	325	−41, −28, 16						
Anterior cingulate	R	3.59	114	9, 29, −6						
Cingulate	R	3.74	624	8, −28, 36						
	L	3.56	279	−3, −14, 36						
Lentiform nucleus	R	3.86	362	30, −8, 2						
	L	4.53	546	−22, −11, 7						
Mediodorsal thalamus	R	3.86	572	9, −19, 3						
Predominantly Sensory (Visual) Processing Regions										
Fusiform gyrus	R	3.81	501	39, −41, −16						
	L	3.77	593	−32, −77, −12						
Lingual/pPHC gyrus	R	4.28	2218	6, −73, 2	4.07	817	21, −65, −2	3.87	2307	12, −90, −14
	L	3.68	1749	−14, −68, −5	3.81	1184	−8, −73, 3	3.66	680	−15, −87, 3
Superior temporal gyrus	R	3.82	325	56, −57, 14						
	L	3.80	1305	−41, −30, 16				3.85	1618	−62, −25, 7
Middle temporal gyrus	L	3.63	456	−41, −61, 14				3.50	1167	−54, −31, 4
Middle occipital gyrus	R				3.80	773	32, −83, 20			
Cuneus	R	4.15	1456	6, −75, 6				3.72	1102	3, −75, 11
	L	3.86	532	−7, −80, 7				3.60	261	−12, −97, 3
Precuneus	R	3.77	1282	8, −62, 43						
	L							3.70	339	−12, −56, 46
V1	R							3.81	497	13, −87, 3
	L							3.63	294	−20, −91, 1
Additional Regions										
Precentral gyrus	R	3.78	629	42, −16, 35						
	L	3.86	838	−43, −17, 34						
Superior parietal lobule	L							3.77	902	−35, −59, 52
Inferior frontal gyrus	L							3.86	633	−43, 11, 29

The mean *t* value for all clusters exceeding threshold for cluster size (248 mm^3) and *p*-threshold (voxel-based $p < .005$ and whole-brain corrected $p < .023$) are presented. For the ACC cluster, the following thresholds were a cluster size of 106 mm^3 with a voxel-based $p < .005$ and ROI corrected $p < .026$. pPHC = posterior parahippocampal gyrus.

circles. As with the downward versus upward triangle comparison, no brain regions showed greater activation for circles compared to downward-pointing triangles.

Circles Compared to Upward-pointing Triangles

Although not central to the understanding of the neural circuitry underlying perception of the downward V-shape, some interesting findings arose in the circle versus upward triangle contrast that are consistent with earlier work (Bar & Neta, 2006; Aronoff et al., 1992) that suggests that circles and curvilinear forms may also be salient visual cues. Whereas upward triangles did not elicit greater activation than circles in any region of the brain, a large number of visual association, visual attention, and other areas were activated by circles (see Table 1). This suggests that circles are a more potent, salient visual stimulus than upward-pointing triangles, a notable finding given that this is the same triangle which robustly recruits a broad range of affect and visual processing areas, but is simply inverted.

Functional Connectivity Analysis: Affective–visual Perception Networks Recruited by Viewing of Downward-pointing V-shape

In light of the existence of widespread cortical projections from the amygdala (Amaral & Price, 2002), and previous work suggesting that the amygdala modulates activity in the ventral visual pathway, including the fusiform gyrus (Vuilleumier et al., 2004; Anderson & Phelps, 2001; Morris et al., 1998), we examined the degree to which amygdala activation in response to the downward V-shape was positively coupled with activation in the fusiform gyrus. To this end, we tested for condition-dependent changes in connectivity (i.e., psychophysiological interaction analysis; Friston et al., 1997). Consistent with previous data indicating amygdalar modulation of fusiform activation, results revealed that this region exhibited increased coupling with the amygdala during the presentation of downward- compared to upward-pointing triangles (Figure 3; $t = 4.42$, [38, −38, −16]). Although the data are consistent with a modulatory role for the amygdala, this kind of analysis cannot provide conclusive evidence on the issue of directionality. Positive coupling with the amygdala BOLD response was also evident in several other regions that showed activation to the downward-pointing triangles, including the subgenual cingulate cortex (see Figure 3), lingual gyrus, and STG. Additional regions demonstrating positive coupling with the amygdala cluster based on the downward compared to upward triangle contrast are presented in Table 2. In general, the connectivity analyses replicate the findings of the initial whole-brain ANOVA and lay the foundation for future work exploring circuitry recruited by the downward V-shape.

DISCUSSION

Amygdala Activation to the Downward-pointing V-shape

These findings support our contention that signals of danger can be represented by a fundamental visual stimulus, specifically a downward-pointing acute angle, thus facilitating efficient detection of threat. The present data are further consistent with arguments made by numerous researchers that evolution has selected for a neural mechanism that permits the rapid detection of threat based on simple stimulus features, and that the amyg-

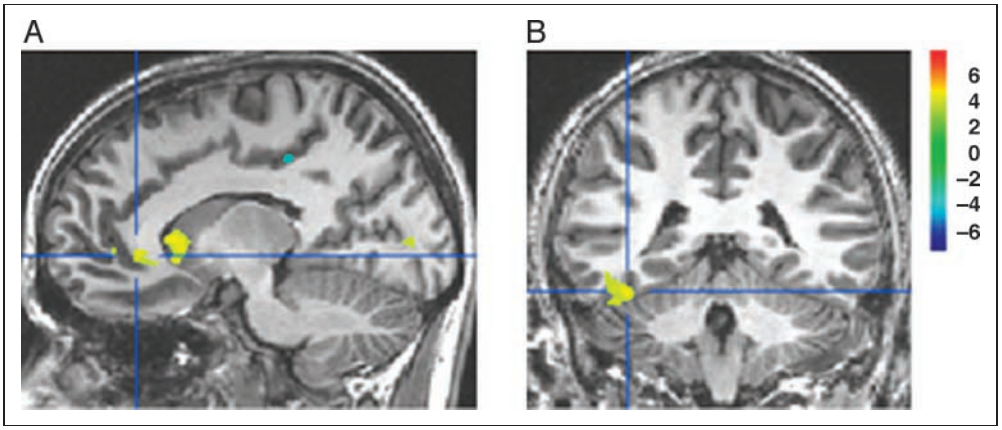

Figure 3. Illustration of greater coupling of amygdala activation with subgenual ACC (A) and fusiform gyrus (B) activity in response to downward triangles compared to upward triangles. A t statistic comparing coupling coefficients for each voxel was calculated. Clusters of 248 mm^3 with a voxel-based p threshold of .005 (a whole-brain corrected p threshold of .023) were considered statistically significant. Orange and red tones indicate greater coupling for downward compared to upward triangles. Images are presented in radiological convention, such that the right side of the image represents the left hemisphere. Greater coupling with amygdala activation was observed for downward triangles compared to upward triangles in both regions. Maximum t value for each cluster and the Talairach coordinates of this value are as follows: subgenual ACC: $t = 4.08$, [12, 31, −1]; right fusiform gyrus: $t = 4.42$, [38, −38, −16]. In each figure, the crosshairs are centered on the coordinates of the peak t value for the downward–upward triangle coupling comparison. Although other regions also showed differential coupling with the amygdala, the focus here is on cortical regions identified in the main analyses to respond to downward triangles.

Table 2. Regions Correlated with Activated Cluster in the Left Amygdala

Region		*Mean t Statistic*	*Volume (mm^3)*	*Coordinates x, y, z*
Anterior cingulate	R	4.08	724	12, 31, −1
Fusiform gyrus	R	4.42	424	38, −38, −16
Caudate/putamen	R	8.61	2725	16, 17, 5
Caudate	L	3.75	356	−18, 14, 2
Prefrontal cortex	R	4.51	441	50, 37, 15
Temporal operculum	R	6.74	2718	60, −5, 5
Superior temporal gyrus	R	4.51	894	45, −27, 7
Middle temporal gyrus	L	4.81	894	−64, −52, 8
Lingual gyrus	R	4.87	265	6, −86, 3
Lingual gyrus	L	4.53	315	−14, −89, −7

All regions from the downward-pointing compared to upward-pointing triangle contrast showing positive coupling with the amygdala cluster demonstrating greater BOLD responses for downward- compared to upward-pointing triangles. Clusters were designated as significant if they exceeded the cluster threshold of 248 mm^3 and the *p*-threshold criteria (voxel-based $p < .005$ and whole-brain corrected $p < .023$).

dala is a key component of this system (Öhman & Mineka, 2001; LeDoux, 2000). Although previous fear conditioning studies in rats have found that an intact amygdala is sufficient to condition animals to very simple stimuli, such as pure tones, even following lesions to the relevant sensory cortex (Doron & LeDoux, 1999), studies in humans have typically assessed the role of the amygdala in responses to contextually laden affective stimuli. However, recent data from multiple sources now suggest that, across multiple sensory modalities, the amygdala is reactive to very simple cues of threat or anger (Whalen et al., 2004; Vuilleumier et al., 2003) including those that have been stripped of associated contextual cues, such as anger prosody (Sander et al., 2005). The present data suggest that the visual stimuli necessary for this recruitment may be even more elemental than previously thought. Previous work demonstrating that schematic faces that include eyebrows in a downward V-shape (Wright, Martis, Shin, Fischer, & Rauch, 2002) and sharp, angular objects (Bar & Neta, 2007) recruit the amygdala have provided hints that the geometric configuration of a stimulus may be linked with recognition of threat. The present findings extend this work in two important ways. First, we show that not only are geometric properties capable of engaging the amygdala but that this process can be reduced even further to a very simple shape. Second, no region in the brain showed greater activation for upward-pointing V-shapes than either the downward-pointing V or the circles. Thus, the present data clearly indicate that not any angular shape is sufficient to convey threat or engage the amygdala and associated brain regions known to underlie negative affect and detection of threat, but that the orientation of the angle is critical.

Although amygdala activation was not observed when contrasting downward-pointing triangles with circles, this lack of differential activation is consistent with behavioral data indicating that circles and curvilinear forms convey the emotion of happiness (Larson et al., 2007; Zebrowitz, 1998; Aronoff et al., 1988) and functional neuroimaging data implicating the amygdala in responses to positively valenced affective stimuli and situations (Britton et al., 2006; Fitzgerald, Angstadt, Jelsone, Nathan, & Phan, 2006; Ernst et al., 2005).

As reported in the Introduction, there is growing evidence from subjective ratings (Larson et al., 2007; Bar & Neta, 2006; Aronoff et al., 1988, 1992), attentional bias (Larson et al., 2007), and neuroimaging (Bar & Neta, 2007) work that cumulatively add to the body of evidence supporting the validity of the downward V-shape as a depiction of threat. Indeed, the regions activated by the downward-pointing V-shape show a striking similarity to those recruited by angular neutral and abstract objects in the study by Bar and Neta (2007). In light of this work and the extensive literature implicating the amygdala in threat-related processes, we have interpreted amygdala activation to downward-pointing triangles as additional evidence supporting the hypothesis that this shape is an effective threat cue.

However, several additional factors need to be considered when interpreting these results. As the amygdala has also been found to be activated by a number of other tasks seemingly unrelated to threat or emotion, such as neutral faces (Fitzgerald et al., 2006), gaze monitoring (Hooker et al., 2003), unpredictable innocuous tones (Herry et al., 2007), and more rapid responses in a working memory task (Schaefer et al., 2006), the mere presence of amygdala activation to the downward-pointing triangles does not, in itself, provide incontrovertible evidence that the downward-pointing V-shape signals threat. Factors such as different patterns of eye movements or attentional orientation may be evoked by these visual forms, and the contribution of such factors to the recognition process should be addressed with future work. Additionally, greater activation to the downward- compared to upward-pointing triangle may be due to the fact that the upward-pointing triangle is a more ''standard'' (or commonly seen) version of the shape, and thus, is less novel. Although this is certainly possible, we have previously found that search times are faster for a downward-pointing V (literally the letter ''V'') than the same shape inverted. As ''V'' is a letter, and thus, the more standard variant of the shape, these findings are not consistent with the novelty interpretation. Finally, it is also possible that the numerosity task used to maintain the participant's attention may be a factor; however, the fact that performance was at ceiling and did not differ as a function of shape suggests that the observed BOLD differences were likely not due to task difficulty.[2]

Activation to the Downward-pointing V-shape in Other Regions

As predicted, we observed increased activation of the ventral visual pathway and other visual cortical regions, including the fusiform gyrus, during viewing of the downward V-shape. The lateral portion of the mid-fusiform gyrus responds strongly to faces (Kanwisher et al., 1997) and its activation is heightened by affective expressions (Kesler-West et al., 2001). Importantly, previous studies using fearful faces as affective stimuli have demonstrated that the amygdala and the fusiform gyrus form a functional network for processing these stimuli, as evidenced by increased coupling of these two regions during viewing of fearful faces (Morris et al., 1998) and the fact that an intact amygdala potentiates responses in the fusiform cortex (Vuilleumier & Pourtois, 2007). The present data indicate that, much like the response to emotional faces, not only does viewing of the downward-pointing V-shape activate the amygdala and a region of the fusiform gyrus that overlaps with the face processing fusiform region but it also enhances connectivity between these two regions. These data further highlight that responses to this simple shape are similar to those recruited by contextually rich affective stimuli, such as affective faces.

With respect to visual cortical regions more generally, as would be predicted by Vuilleumier's model of affect modulation of visual processing (Vuilleumier & Driver, 2007), we found widespread increases in activation in regions of the ventral visual pathway and visual attention areas for the downward-pointing triangles compared to the other shapes. Interestingly, we also found that circles were more potent activators of these regions than the upward-pointing triangles, albeit to a lesser extent than the downward-pointing triangles. On the premise that activation in visual cortical regions is potentiated by attention-grabbing and affective stimuli (Vuilleumier & Driver, 2007), these data are once again consistent with previous behavioral work demonstrating that downward-pointing V and circular forms convey emotion (Larson et al., 2007; Bar & Neta, 2006; Aronoff et al., 1988, 1992). The augmented activation associated with the threat-related shape compared to the happiness-related shape in these affect-modulated visual regions is further in keeping with previous work identifying a negativity bias, such that negatively valenced information receives preferential processing (Cacioppo, 1994).

Another region with face- and affect-sensitive response properties, the superior temporal gyrus and sulcus (Allison, Puce, & McCarthy, 2000) (STG/STS), showed greater activation for both of the affective shapes, the downward triangle and the circle. Activation in the STG/STS is elicited by viewing of faces, facial features (Puce, Allison, Bentin, Gore, & McCarthy, 1998), and emotional faces (Phillips et al., 1998), including those depicting anger (Hooker et al., 2003). The STG has also been found to be responsive to biologically meaningful eye gaze direction (Hooker et al., 2003). In addition to the face, the STG has also repeatedly been found to be engaged during viewing of biological motion, both when watching real human movement (Allison et al., 2000) and when viewing point-light representations of movement (Bonda, Petrides, Ostry, & Evans, 1996). Importantly for the present work, this STG activation to biological motion has been found to depend upon processing of the configural aspects of the stimulus (Thompson, Clarke, Stewart, & Puce, 2005). Relatedly, Downing, Jiang, Shuman, and Kanwisher (2001) identified a region of the STG that responds preferentially to images of the human body, including simple graphic forms, such as stick figures and silhouettes. Notably, previous work examining the configural bases of emotion found that angular patterns of body movement and position are perceived as threatening (Aronoff et al., 1992). Further reinforcing the notion that the STG responds to simple and fundamental biologically relevant cues, voice prosody during angry nonsense speech also activates this region (Grandjean et al., 2005). Thus, the STG appears to be broadly activated by biological signals from the face and the body (Allison et al., 2000), and is responsive to cues representing the configural forms underlying these signals. The fact that the STG is robustly activated by affective and biologically relevant stimuli has led some researchers to suggest that the STG is an important node in the neural circuitry underlying social cognition (Adolphs, 2002). With respect to our findings, activation of this region in response to configural shapes associated with emotion further underscores their potential role as fundamental cues of biologically relevant information.

In addition to the amygdala, several other regions repeatedly implicated in emotion-related processes were activated by downward-pointing V's, but not to either of the other shapes. Activation of the subgenual ACC in response to the downward-pointing V-shape is consistent with previous work indicating that this shape carries a connotation of negative affect. The ACC has been implicated in a wide range of affective and cognitive functions, with the ventral portion, including the subgenual ACC, predominantly demonstrating sensitivity to affect-related processes (Bush, Luu, & Posner, 2000). Negative affect (NA), in particular, has been linked with activation of this region, both in terms of induced negative mood (Liotti et al., 2000) and more trait-like cases of NA, including self-reported high-trait NA (Zald, Mattson, & Pardo, 2002) and major depressive disorder (Drevets et al., 1997). In addition to increased activation, we also found positive coupling of activation in the amygdala and the ventral ACC during viewing of downward- compared to upward-pointing triangles, again implicating an amygdalar–cortical network in perception of this shape. Although initial work on the role of the ventral ACC in emotion focused more on the pathogenesis of mood pathology (Drevets et al., 1997), these data also underscore the role of this region in processing of stimulus-driven negative affect, including simple context-free representations of threat.

The insular cortex has been implicated in a broad range of functions including visceral responses, responding to other's facial expressions (Carr, Iacoboni, Dubeau, Mazziotta, & Lenzi, 2003), pain (Sawamoto et al., 2000), and a number of unpleasant emotions (Phillips et al., 1998). Interestingly, another pain-responsive region in the cingulate cortex (Sawamoto et al., 2000; Rainville, Duncan, Price, Carrier, & Bushnell, 1997) also showed increased BOLD response to the downward V-shape. Although we have not conceptualized the downward V form as being explicitly related to pain, the experience and expectancy of pain is clearly amplified by unpleasant emotional states and threat stimuli (Rainville et al., 1997), and thus, may be part of the larger affective processing network that instantiates recognition of and preparation for responses to potential threat.

Caveats

The present work certainly does not deny the important effects of contextual cues in eliciting affect and perception of threat; nor does it suggest that other attributes of a particular stimulus, such as size (Tipples, 2007), are unimportant. Furthermore, this work is not meant to suggest that all visual depictions of threat are based on the V-shape. Rather, these data highlight the fact that it is possible for visual depictions of threat to be reduced to a simple geometric configuration. In addition, although the spatial resolution of the imaging data does not permit conclusions at the cellular level, given the potential biological relevance of this shape, it is intriguing to speculate that there may be specific cells (or sets of cells) which are tuned to respond primarily to the downward acute angle, just as there are cells known to respond to diagonal lines and other geometric forms (Livingstone & Hubel, 1988).

Summary

In sum, consistent with the notion that simple, repeatable patterns aid in efficient detection of threat (Herry et al., 2007), the current data provide additional support for the idea that visual threat can be conveyed by a simple downward V-shape, even when completely devoid of other contextual or affective cues. Recognition of this shape is instantiated in a network of regions previously implicated in the processing of contextually rich affective and biologically relevant stimuli, such as threat-related faces, including the amygdala, the subgenual ACC, the STG/STS, and the fusiform gyrus. This pattern of activation supports the findings from our previous behavioral studies indicating that the downward V-shape operates as a signal of threat, both at a subjective and attentional level. Recognition of this configural representation is likely facilitated by the amygdala and the STG/STS, with the amygdala then eliciting heightened processing in visual sensory regions. Importantly, these results suggest that this neural circuitry may achieve efficient recognition of threat through detection of the underlying geometry of the stimulus. Thus, the essence of visual threat can be signaled and detected based on far less stimulus information than previously demonstrated to be necessary.

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Notes

1. In a Shape (downward triangle, upward triangle, circle) × Numerosity (1, 2, 3, 4, 5, 7) repeated measures ANOVA, the main effect for shape was not significant ($F < 1$; means: downward triangle = 651.88 msec, upward triangle = 653.41 msec, circle = 649.72 msec). There was a significant main effect for numerosity [$F(5, 95) = 19.07$, $p < .001$]. Subsequent analyses revealed that participants took longer to determine that fewer than four shapes were present (mean of 1–3 shapes = 661.18) than greater than four [mean of 5–7 shapes = 631.27; $t(19) = 4.50$, $p < .001$]. This finding was primarily driven by the fact that the two conditions closest to the choice point (4 shapes) were the most difficult distinctions to make. In particular, responses to the condition in which three shapes were presented were slower than all other numerosity conditions (ps < .05), including the five-shape condition.

2. A Shape × Numerosity ANOVA, in which numerosity was composed of two factors (1–3 or 5–7 shapes), was calculated

on a voxelwise basis. Importantly, no Shape × Numerosity interaction was present for any of the affect-related regions reported in the main analysis. Three regions did show significant interactions surviving cluster threshold. Both the left lingual gyrus (−10, −89, 11; 2683 voxels) and the left posterior cingulate/precuneus (−19, −15, 14; 703 voxels) showed greater activation for more compared to fewer shapes for upward-pointing triangles. Also, the right cuneus (17, −72, 9, 944 voxels) showed an advantage for more compared to fewer shapes for the downward-pointing triangle.

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