Looming animate and inanimate threats: The response of the amygdala and periaqueductal gray

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Abstract

Looming stimuli are processed as threatening and activate basic neural defense systems. However, it is unclear how animacy information modulates this response. Participants (N = 25) viewed threatening or neutral images that were either animate (animals) or inanimate (objects) and which either approached (loomed) or receded from the participant. The amygdala was responsive to emotional, animacy and looming information (particularly to looming threats and looming animate stimuli). Periaqueductal gray was also sensitive to emotional information and particularly responsive to looming threats. The data are interpreted within category specific models of the amygdala and temporal cortex.

Keywords

Amygdala; Animacy; Threat; Looming; Periaqueductal Gray

Introduction

Considerable animal work has examined defensive responses to threat (Gregg & Siegel, 2001; Panksepp, 1998). This response is mediated via a circuit that runs from the medial amygdala downward, largely via the stria terminalis to the medial hypothalamus, and from there to the dorsal half of the periaqueductal gray (PAG: Gregg & Siegel, 2001; McNaughton & Corr, 2004; Panksepp, 1998). Ventromedial prefrontal cortex is thought to play a role in the modulation of these defensive responses (R. J. R. Blair, 2004; Price, 1999, 2007). Several recent studies have explored defensive reactions to threat in humans (Mobbs et al., 2009; Mobbs et al., 2007; Mobbs et al., 2010). These studies have used threat situations involving pursuit in the context of a computer game (where capture meant receiving shock; Mobbs et al., 2009; Mobbs et al., 2007) or a spider apparently approaching or withdrawing from the participant's foot (Mobbs et al., 2010). They have shown that imminent threat is associated with increased amygdala and PAG activity and reduced

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ventromedial prefrontal cortex activity while more distal threats are associated with increased vmPFC and reduced PAG activity (Mobbs et al., 2009; Mobbs et al., 2007; Mobbs et al., 2010).

Threats become more intense as they get closer (Blanchard, Blanchard, & Takahashi, 1977). Indeed, it is believed that rapidly looming stimuli trigger defensive behaviors. However, the effect of animacy information on the activation of defense systems by apparent decreasing proximity or, for that matter, emotional threat level remains unclear. Previous fMRI work examining defensive responding has examined animate stimuli (e.g., spiders or pursuing avatars whose behavior was contingent on that of the participant; Mobbs et al., 2009; Mobbs et al., 2007; Mobbs et al., 2010). Yet psycho-physiological work indicates that conditioned responses are more readily learned, and more resistant to extinction, in response to animate threats relative to inanimate threats (Mineka & Zinbarg, 2006). It is possible that defensive responding is only shown to animate threats. Certainly, the amygdala shows increased responsiveness to animate relative to inanimate stimuli as well as to emotional relative to neutral stimuli (Gobbini et al., 2011; Martin & Weisberg, 2003; Santos et al., 2010; Wheatley, Milleville, & Martin, 2007). Moreover, there have been some indications that the amygdala – a core component of the defensive threat circuitry – only responds to animate, and not inanimate, threats (Yang, Bellgowan, & Martin, 2013). Thus, the first goal of this study was to determine whether the recruitment of defensive threat circuitry would be seen for simple looming stimuli and the degree to which this response might be modulated by emotional and animacy information. Our second goal was to investigate the functional significance of the amygdala response to looming emotional and animate stimuli. Further, we wished to determine whether any recruitment of additional systems implicated in the defensive response to threat (e.g., PAG) might show differential activity to animate relative to inanimate stimuli as well as threatening relative to neutral stimuli or whether PAG responsiveness is contingent on the threat content of the stimulus.

We investigated this issue with a novel paradigm. In this paradigm, the participant was presented with images that either appeared to loom towards, or recede from, them (as a consequence of rapid changes in the visual angle of the stimulus). The images were distinguished by animacy (animate vs. inanimate) and emotion (threatening vs. neutral). Three predictions were made. First, following previous work on the neural responses to animacy (Yang et al., 2013) and emotional information (Zald, 2003), we predicted that the amygdala would show significant responses to both emotional (threatening) and animate stimuli. Second, following previous work (Mobbs et al., 2009; Mobbs et al., 2007; Mobbs et al., 2010), we predicted that the amygdala and PAG would show significant responses to looming relative to receding stimuli. Third, we predicted that either vmPFC (Mobbs et al., 2009; Mobbs et al., 2007) and/or more lateral regions of orbital frontal cortex (Mobbs et al., 2010) would show reduced responsiveness to threat, particularly looming threat.

Method

Participants

Twenty-five right-handed participants (16 males, 9 females; aged 21–45, mean age = 27.08) volunteered for the study and were paid for their participation. Participants were in good physical health as confirmed by a complete physical exam, with no history of any psychiatric illness as assessed by the DSM-IV (1994) criteria based on the Structured Clinical Interview for DSM-IV Axis I Disorders (SCID; First, Spitzer, Gibbon, & Williams, 1997). All participants gave written informed consent to participate in the study, which was approved by the National Institute of Mental Health Institutional Review Board.

Looming Task

The looming task involved the presentation of four different types of images: (i) threatening and animate (e.g. snarling dogs); (ii) threatening and inanimate (e.g. pointed gun); (iii) neutral and animate (e.g. sitting rabbit); or neutral and inanimate (e.g. a mug). All animate stimuli were animals and all inanimate stimuli were objects presented on their own (i.e., no hand was holding the gun/mug). The stimuli were taken from previous work (Yang et al., 2013). In that study, participants rated each item's valence and arousal. We took a sample of stimuli from this set. However, within our stimulus set, animate stimuli were significantly more arousing than inanimate stimuli (though considerably less so than the difference between threatening and neutral stimuli; t=2.94 vs. t=21.43; p<0=0.004 vs. p=0.000). As planned, while threatening stimuli were more negatively valenced than neutral stimuli, animate stimuli were not more negatively valenced than inanimate stimuli (t=19.83 vs. 1.27; p<0.000 vs. n.s.).

Each trial involved the *rapid presentation of the same image 4 times* (250ms per presentation). Each presentation involved the image taking up a greater (or lesser) extent of the screen. Thus, for *looming trials*, centered images occupied 25%, then 50%, then 75% and then 100% of the screen. For *receding trials*, centered images occupied 100%, then 75%, then 50% and then 25% of the screen (see Figure 1). Following these presentations was a 1250ms fixation. Participants simply had to respond via button press as soon as they perceived the image. The task involved 4 runs of 5 minutes and 59 seconds, each consisting of 80 image trials (20 of each of the 8 trial types) and 60 2000ms fixation trials.

fMRI Data Acquisition and Preprocessing

Whole-brain blood oxygen level dependent (BOLD) fMRI data were acquired using a 3.0 Tesla GE MRI scanner. Following sagittal localization, functional T2* weighted images were acquired using an echo-planar single-shot gradient echo pulse sequence (matrix = 64 X 64 mm, repetition time (TR) = 2900 ms, echo time (TE) = 27 ms, field-of-view (FOV) = 22cm (3.43x3.44mm). Images were acquired in 44 2.5mm axial slices with .5mm spacing per brain volume over 4 runs with each run lasting 5 minutes 59 seconds. A high-resolution anatomical scan (3-dimensional spoiled gradient recalled acquisition in a steady state; repetition time=7 milliseconds; echo time=2.984 milliseconds; 24cm field of view; 12° flip angle; 128 axial slices; thickness, 1.2 mm; 256x192 matrix) in register with the EPI data set was obtained covering the whole brain.

Imaging data preprocessing

Data were analyzed within the framework of the general linear model using Analysis of Functional Neuroimages (AFNI; Cox, 1996). Both individual and group-level analyses were conducted. The first five volumes in each scan series, collected before equilibrium magnetization was reached, were discarded. Motion correction was performed by registering all volumes in the EPI dataset to a volume collected close to acquisition of the high-resolution anatomical dataset.

The EPI datasets for each participant were spatially smoothed (isotropic 6 mm kernel) to reduce variability among individuals and generate group maps. Next, the time series data were normalized by dividing the signal intensity of a voxel at each time point by the mean signal intensity of that voxel for each run and multiplying the result by 100, producing regression coefficients representing percent-signal change.

Following this, the following eight regressors were generated: (i) looming, threatening, animate; (ii) looming, threatening, inanimate; (iii) looming, neutral, animate; (iv) looming, neutral, inanimate; (v) receding, threatening, animate; (vi) receding, threatening, inanimate;

(vii) receding, neutral, animate; (viii) receding, neutral, inanimate. These eight regressors were created by convolving the train of stimulus events with a gamma-variate hemodynamic response function to account for the slow hemodynamic response. Linear regression modeling was performed using the 8 regressors described above plus 6 head motion regressors. This produced a modulated and un-modulated β coefficient and associated *t* statistic for each voxel and regressor. Voxel-wise group analyses involved transforming single participant beta coefficients into standard coordinate space (Talairach & Tournoux, 1988).

fMRI data analysis

The BOLD data were analyzed via a 2 (Direction: Looming, Receding) by 2 (Emotion: Threatening, Neutral)×2 (Animacy: Animate, Inanimate) ANOVA. Given previous work and our a priori hypotheses, regions of interest (ROIs) were created. Given the well-defined anatomical boundaries of the amygdala, an anatomical ROI was taken from the AFNI software. ROIs for vmPFC and PAG were constructed by creating a sphere with a 10mm radius around peak voxels from previous work (Mobbs et al., 2010): vmPFC: −4,50, −9; PAG: 8, −26, −5. A small volume-corrected ROI analysis was conducted for these regions using ClustSim (initial threshold: p<0.005 [except within the amygdala; p<0.05] corrected at p<0.05 for the number of voxels within the ROI). To facilitate interpretation of these results, the average percent signal change was quantified within each functional ROI so that mean values for each event type in each participant could be extracted and group-level statistics performed within SPSS.

For completion, a whole-brain analysis was also conducted using a 2 (Direction: Looming, Receding) by 2 (Emotion: Threatening, Neutral)×2 (Animacy: Animate, Inanimate) repeated measures ANOVA. All regions were corrected for multiple comparisons via ClustSim (initial threshold: p=0.005 corrected at p=0.05 using an extent threshold of 42.7 voxels). Group effects were masked using a brain mask based on the mean normalized anatomical images of all participants.

Results

A 2 (Direction: Looming, Receding) by 2 (Emotion: Threatening, Neutral)×2 (Animacy: Animate, Inanimate) ANOVA was conducted on participant response latencies revealing a significant main effect for direction [F(1,24)=6.704, *p*=.016] where participants responded more quickly to looming relative to receding stimuli. There were no other main effects or significant interactions.

fMRI Results

A 2 (Direction: Looming, Receding) by 2 (Emotion: Threatening, Neutral)×2 (Animacy: Animate, Inanimate) ANOVA was conducted on the participants' BOLD responses within the amygdala, PAG and vmPFC ROIs (see Table 1). A whole brain analysis was also conducted using a 2 (Direction: Looming, Receding) by 2 (Emotion: Threatening, Neutral) ×2 (Animacy: Animate, Inanimate) ANOVA (see Table 2).

Amygdala—In line with predictions, there were significant main effects of emotion (threatening>neutral: left: −23, −4, −16), animacy (animate>inanimate: left: −19, −5, −12; right: 28, −5, −13) and direction (looming>receding: left: −22, −5, −19; right: 27, −4, −22) within the amygdala; see Figure 2. There were also significant direction-by-emotion and direction-by-animacy interactions. With respect to the direction-by-emotion interaction, left amygdala (−22, −8, −12) showed significantly greater increase in responses to threatening approaching relative to threatening receding stimuli than to neutral approaching relative to

neutral receding [$t(24)$=2.807, p=.010]. With respect to the direction-by-animacy interaction, right amygdala (27, −4, −16) showed significantly greater responses to animate approaching relative to animate receding [$t(24)$=3.149, p=.004], while inanimate approaching and inanimate receding trials did not differ [$t(24)$=-.804, p=.429].

PAG—In line with predictions, there was a significant main effect of emotion (threatening>neutral: 4, −29, −2) within the PAG; see Figure 3. In addition, there was a significant direction-by-emotion interaction (8, −32, −8); looming threats were associated with significantly greater activity than receding threats [$t(24)$=2.969, p=.007] and looming neutral stimuli [$t(24)$=2.857, p=.009]. However, there were no main effects of either Looming or Animacy within PAG.

vmPFC—There were no significant main effects or significant interactions within the vmPFC ROI.

Whole brain analysis—The whole brain analysis identified regions of occipital and posterior temporal cortex that showed some overlap (see Table 2 and Figure 4). These regions showed main effects for direction (looming>receding), animacy (animate>inanimate), and emotion (threatening>neutral) as well as an emotion-by-animacy interaction. Within the region showing a significant emotion-by-animacy interaction, the response to threatening or neutral animate stimuli did not differ [$t(24)$=1.37, *n.s.*]. However, the response to both threatening or neutral animate stimuli was significantly greater than the response to threatening or neutral inanimate stimuli [$t(24)$=2.30 to 13.04, p<.001] except threatening animate relative to threatening inanimate stimuli [$t(24)$=2.05, p=.051]. Within this region the response to threatening inanimate stimuli was significantly greater than that to neutral inanimate stimuli [$t(24)$=7.68, p<.001]; see Figure 4. There was also a region of middle temporal gyrus that showed a main effect of animacy (inanimate>animate).

Discussion

The purpose of the current study was to determine whether the activation of defense systems would be seen to simple looming stimuli and the degree to which this response might be modulated by emotion and animacy information. There were three main findings. First, regions of the amygdala showed increased responses to direction (looming>receding), emotion (threatening>neutral) and animacy cues (animate>inanimate). Second, there were significant direction-by-emotion and direction-by-animacy interactions within the amygdala. The amygdala showed significantly increased responding to looming threat relative to receding threat than to looming neutral stimuli relative to receding neutral stimuli (which did not significantly differ). Similarly, the amygdala showed significantly increased responding to looming animate relative to receding animate than to looming inanimate relative to receding inanimate (which again did not significantly differ). Third, PAG showed greater responses to threat relative to neutral stimuli particularly when these threat stimuli were looming.

There have been claims that the amygdala is part of the domain-specific circuitry for responding to animate entities (Adolphs, 2009; Yang et al., 2013). The main effect of animacy within the amygdala seen here is consistent with this view. However, the amygdala also showed a significant main effect for emotion. There was significantly greater responding within the amygdala for threatening stimuli relative to neutral stimuli. These data indicate that the amygdala also shows significant sensitivity to threatening emotional stimuli irrespective of their animacy.

Interestingly, aversive conditioning occurs more readily to evolutionary-relevant animate entities (conspecific and heterospecific) than to equally threatening, but manmade, modern objects (cf. Mineka & Ohman, 2002; Ohman & Mineka, 2001). The amygdala is critically involved in aversive conditioning (e.g., Johansen, Cain, Ostroff, & LeDoux, 2011). It is possible that the differential conditionability of animate relative to inanimate stimuli reflects basic differential responsiveness of the amygdala to these stimuli categories; i.e., the amygdala may more readily form associations of reinforcement with animate stimuli because animate stimuli are more likely to be represented by the amygdala.

Looming objects are perceived as threatening. In line with this (cf. Mobbs et al., 2010), looming stimuli were associated with significantly increased amygdala responses. Interestingly, the data here indicate that the amygdala response to looming stimuli is modulated by emotion *and* animacy information. Regions within the amygdala showed particularly marked responses to approaching threats and approaching animate stimuli. It is unsurprising that the amygdala is particularly responsive to approaching threats, its role in the circuitry mediating the defensive response to threat (cf. Gregg & Siegel, 2001; Panksepp, 1998) should demand this. However, it is interesting that the amygdala is particularly responsive to approaching animate stimuli. There is evidence that aversive conditioning occurs more readily to evolutionary-relevant animate entities than to equally threatening, but manmade, modern objects (cf. Mineka & Ohman, 2002; Ohman & Mineka, 2001). It is perhaps plausible that basic threat behaviors (flight-fight) and the activation of the circuitry mediating them (particularly the amygdala) also occur more readily to evolutionary-relevant animate entities than to equally threatening, but manmade, modern objects.

Previous work has shown increased PAG activity in response to looming threats (spiders apparently approaching the participant's foot and approaching artifical predators who can induce electric shocks; Mobbs et al., 2009; Mobbs et al., 2007; Mobbs et al., 2010). The current study replicates this previous work with a very simple manipulation – images that appear to loom as a function of increasing visual angle. Threats, particularly when they were looming, were associated with increased responses within the PAG. Neutral images did not have this impact.

Previous work has reported that imminent threat is associated with increased amygdala and PAG activity and reduced ventromedial prefrontal cortex activity while more distal threats are associated with increased vmPFC and reduced PAG activity (Mobbs et al., 2009; Mobbs et al., 2007; Mobbs et al., 2010). In the current study, participants showed increased amygdala and PAG activity to threats, particularly approaching threats. However, in contrast to predictions there were no indications of reduced vmPFC activity. The reason for this inconsistency with previous work is unclear. However, it may reflect the relatively benign nature of the threat stimuli here. In the previous work, the threat stimuli have been tarantula spiders apparently approaching the participant's foot or pacman-like artificial predators who, if they "catch" the participant deliver shocks (Mobbs et al., 2009; Mobbs et al., 2007; Mobbs et al., 2010).

In addition to our main regions of interest, our whole brain analysis identified large regions of occipital and posterior temporal cortex that showed main effects for direction (looming>receding), emotion (threatening>neutral) and animacy (animate>inanimate) as well as an emotion-by-animacy interaction. With respect to the animacy main effect, these findings were consistent with previous reports (e.g., Chao, Weisberg, & Martin, 2002). Thus, the large region of visual and temporal cortex which showed a main effect of animacy included all the regions implicated by Chao et al (2002) as responsive to animals (except right superior temporal sulcus). In addition, the region of middle temporal cortex that also

showed a main effect of animacy (inanimate > animate) is proximal to a region identified by Chao et al (2002) as processing inanimate items (tools). The region of visual and temporal cortex which showed a main effect of emotion (threatening > neutral) includes almost all of the regions implicated by Chao et al (2002) as processing animate items as well as the bilateral medial fusiform gyrus implicated in the response to tools. This activity may reflect amygdala driven priming of the representation of emotional stimuli (cf. Pessoa, Kastner, & Ungerleider, 2002). The regions of occipital lobe identified by Chao et al (2002) as showing a main effect of animacy and which also showed main effects of animacy and emotion here also showed an animacy-by-emotion interaction. They were particularly unresponsive to inanimate neutral stimuli (see Figure 4). Interestingly, the main effect of direction implicated more anterior regions of lateral and medial fusiform gyrus (these regions also showed a main response to emotion). These regions were identified by Chao et al (2002) as responsive to animals and tools respectively. The lateral regions of fusiform gyrus also showed greater responses to animals than objects here. However, medial fusiform gyrus did not show greater responses to inanimate objects in the current study. The reasons for this are unclear.

It is worth considering the implications of the paradigm and these results for patients with clinical conditions, particularly patients with anxiety disorders and conduct disorder. Patients with post traumatic stress disorder (PTSD) show an increased risk for reactive aggression (e.g., Silva, Derecho, Leong, Weinstock, & Ferrari, 2001). Reactive aggression is mediated by basic threat circuitry including the amygdala and PAG (Panksepp, 1998; Siegel, Roeling, Gregg, & Kruk, 1999). Previous work has reported increased amygdala responses to threat in patients with PTSD (Rauch, Shin, & Phelps, 2006). It would be interesting to determine whether patients with PTSD also show heightened PAG responses to (looming) threat that might underpin their increased propensity for reactive aggression. Patients with generalized social phobia (GSP) show heightened amygdala responsiveness to emotional expressions (K. S. Blair et al., 2008). It remains unclear whether they show heightened responsiveness to non-social emotional stimuli. As such, it is unclear whether they have a heightened amygdala response to animacy information in addition to, or alternatively to, a heightened response to social threat stimuli. Finally, and most particularly interesting from our own labs' perspective, is the case of conduct disorder (CD). Patients with CD, particularly those with callous-unemotional traits (reduced guilt and empathy), show reduced amygdala responses to fearful expressions and other threat stimuli (Marsh et al., 2008; White et al., 2012). However, the computational details of this insensitivity remain unknown. It will be interesting to determine whether there is reduced modulation of this amygdala response by stimulus direction (looming/receding) and particularly by animacy information. Should modulation of amygdala responsiveness by animacy be detected in this population it would imply that sensitivity of the amygdala more generally (not just emotional responsiveness) is disrupted in patients with CD.

Two limitations should be mentioned with respect to the current results. First, as trials involved the rapid presentation of images that either loomed (covered greater amounts of the screen) or receded, we cannot be certain that the response to looming reflects a response to the stimulus "approaching/receding" or to it taking up a greater or lesser extent of the screen. Of course, somewhat mitigating this concern is the fact that both looming and receding trials involved the same extents of the screen being covered (20, 50, 75 and 100%). Given this, we assume that PAG is responsive to looming threat rather than just close threat. However, it is possible that the effect is driven by the time course of the presentation of the close threat. Future studies might contrast looming threats with static threats that are either close (100% of the screen) or distant (25% of the screen). Second, the animate items were judged to be more negatively valenced and arousing than the inanimate items. This could suggest that the observed amygdala response to animate items reflected only their increased

emotional value rather than animacy information. Somewhat mitigating this concern however is our finding that participants' parameter estimates for the main effect of animacy within the amygdala were greater than those seen for the main effect of emotion [$t=1.916$, $p=.067$]. Such a result would not be predicted if the amygdala was only responsive to emotional information.

In summary, the current study indicates that defensive responding is shown to looming stimuli particularly when these stimuli are either threatening or animate. In short, while there is a general defensive reaction to looming stimuli, this is particularly marked for threatening and animate looming stimuli. This suggests that basic threat behaviors (flight-fight) and the activation of the circuitry mediating them (particularly the amygdala) occurs more readily to evolutionary-relevant animate entities than to equally threatening, but manmade, modern objects.

Acknowledgments

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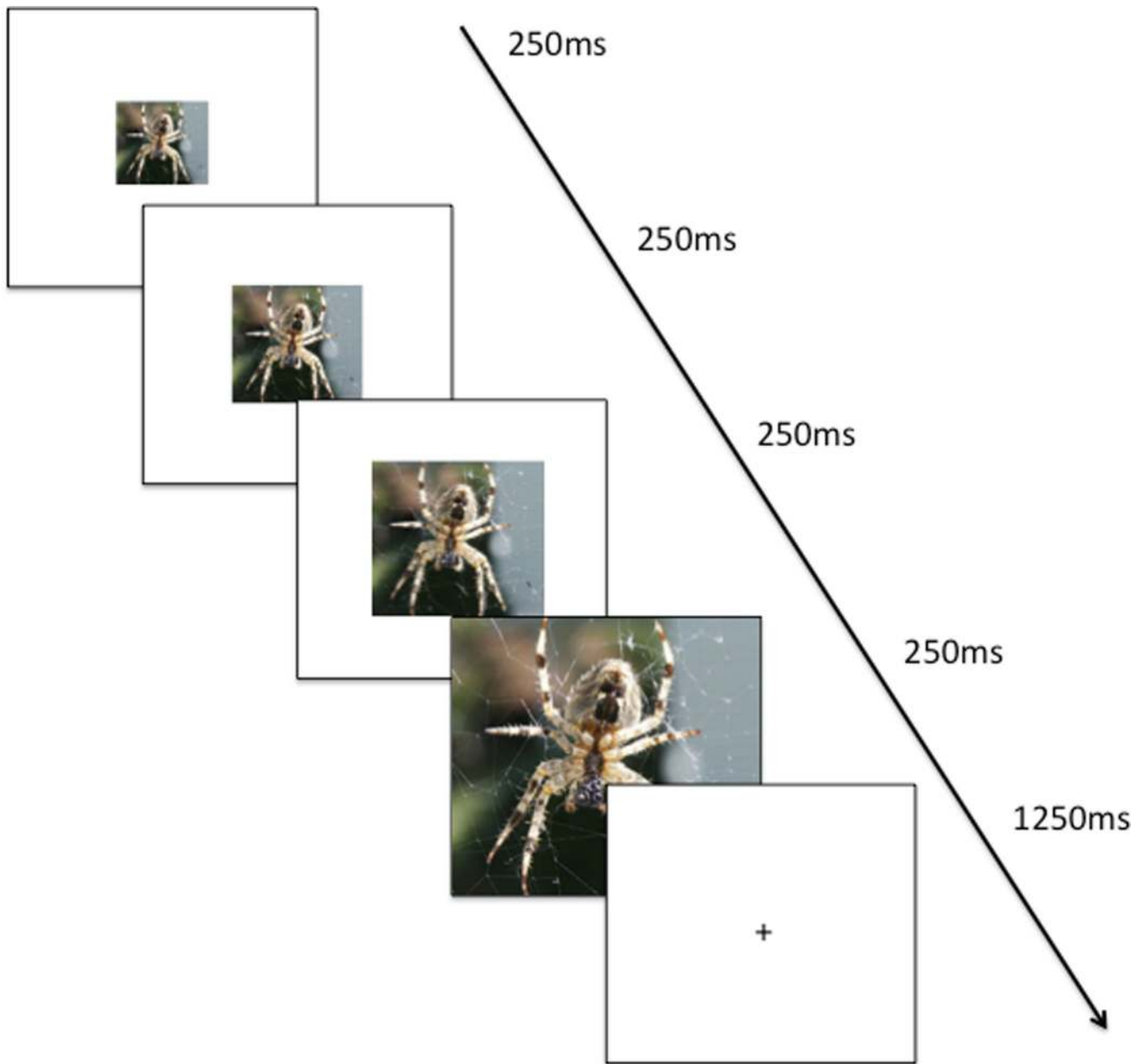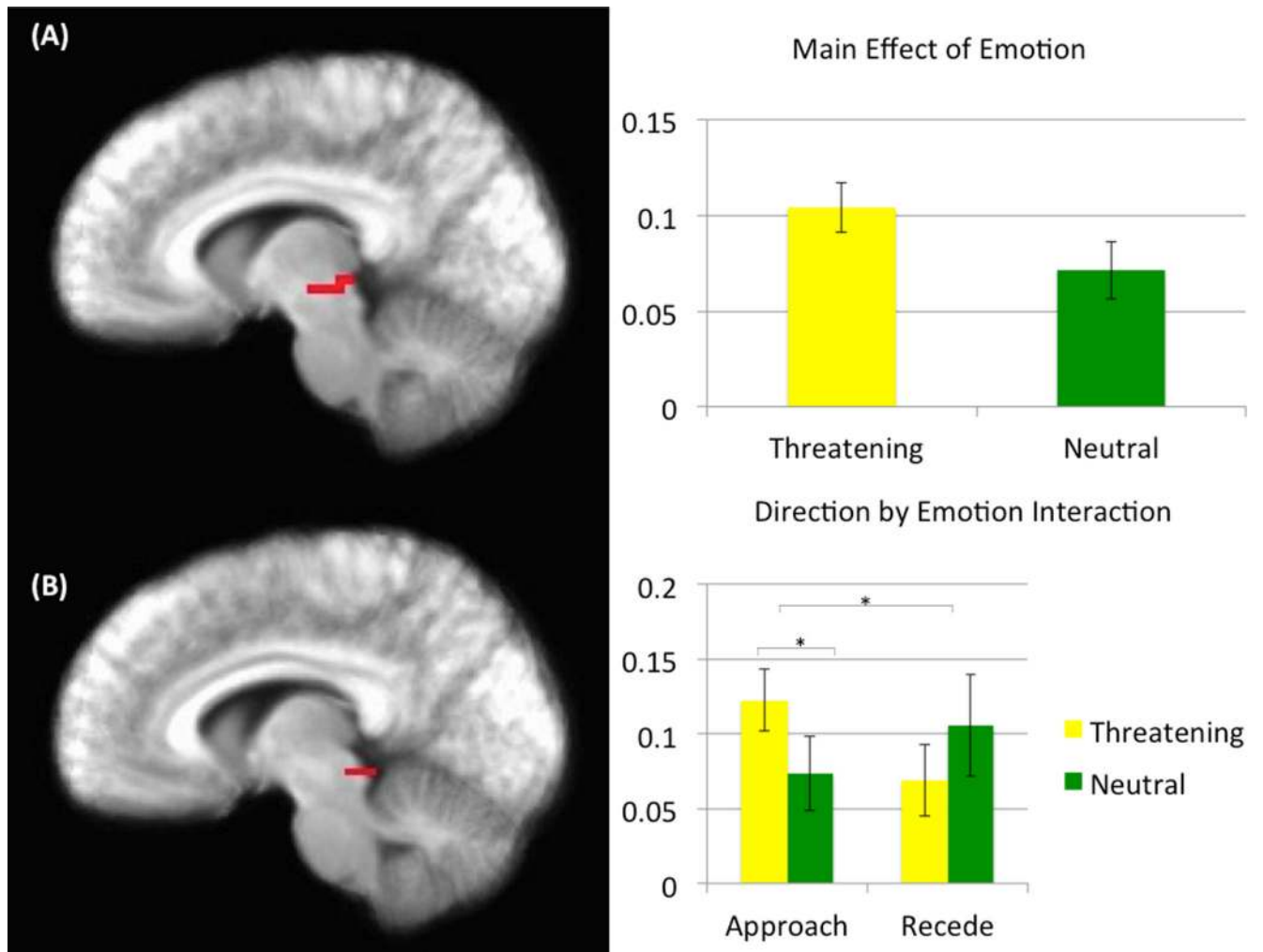
Figure 1.
The Looming task.
On each trial, participants received a serial presentation of images that either increased in visual angle (i.e., a looming trial, depicted in the figure) or receded. Images could be either animate or inanimate and threatening or neutral. Participants responded via button press when they saw an image.
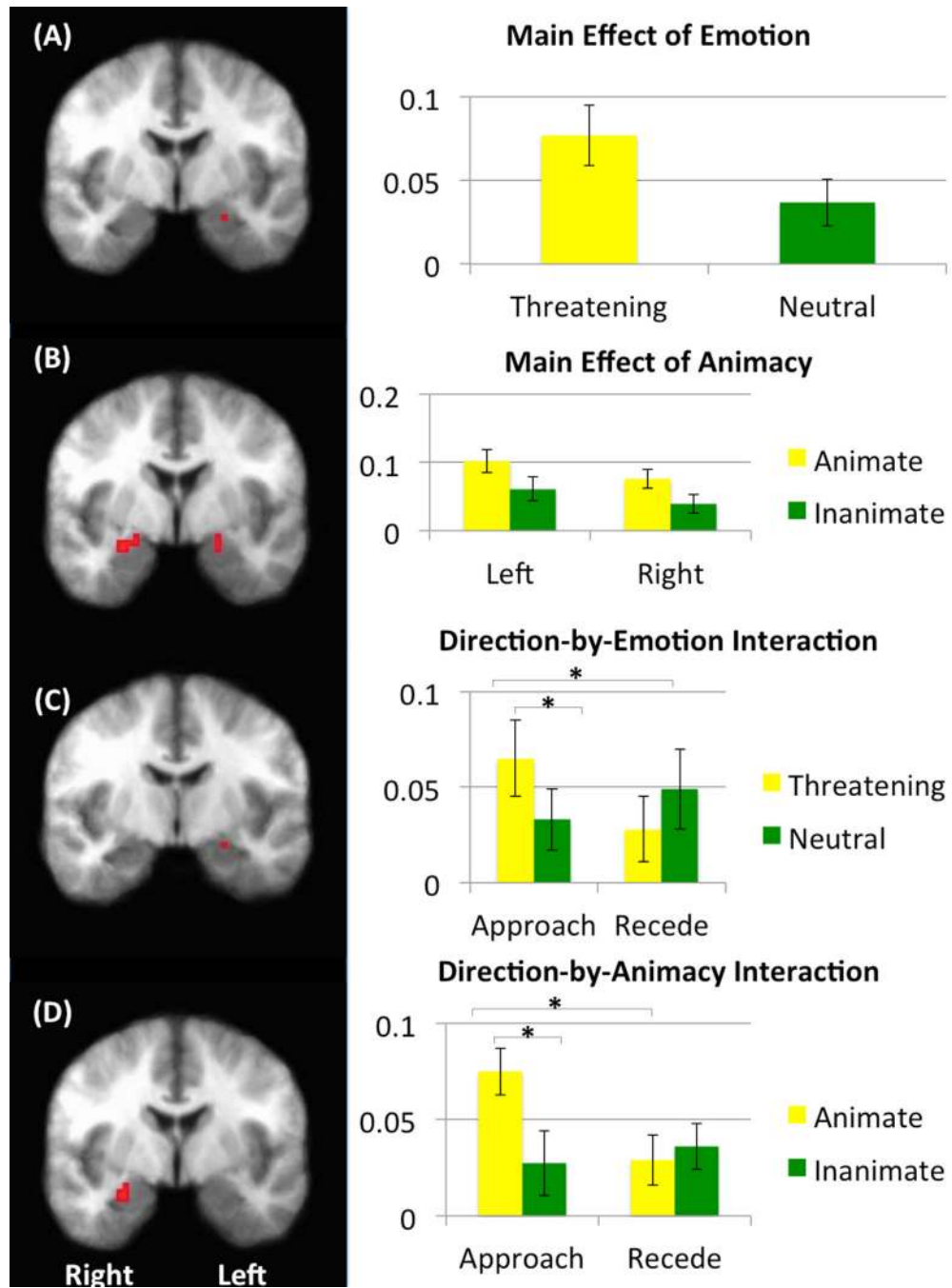
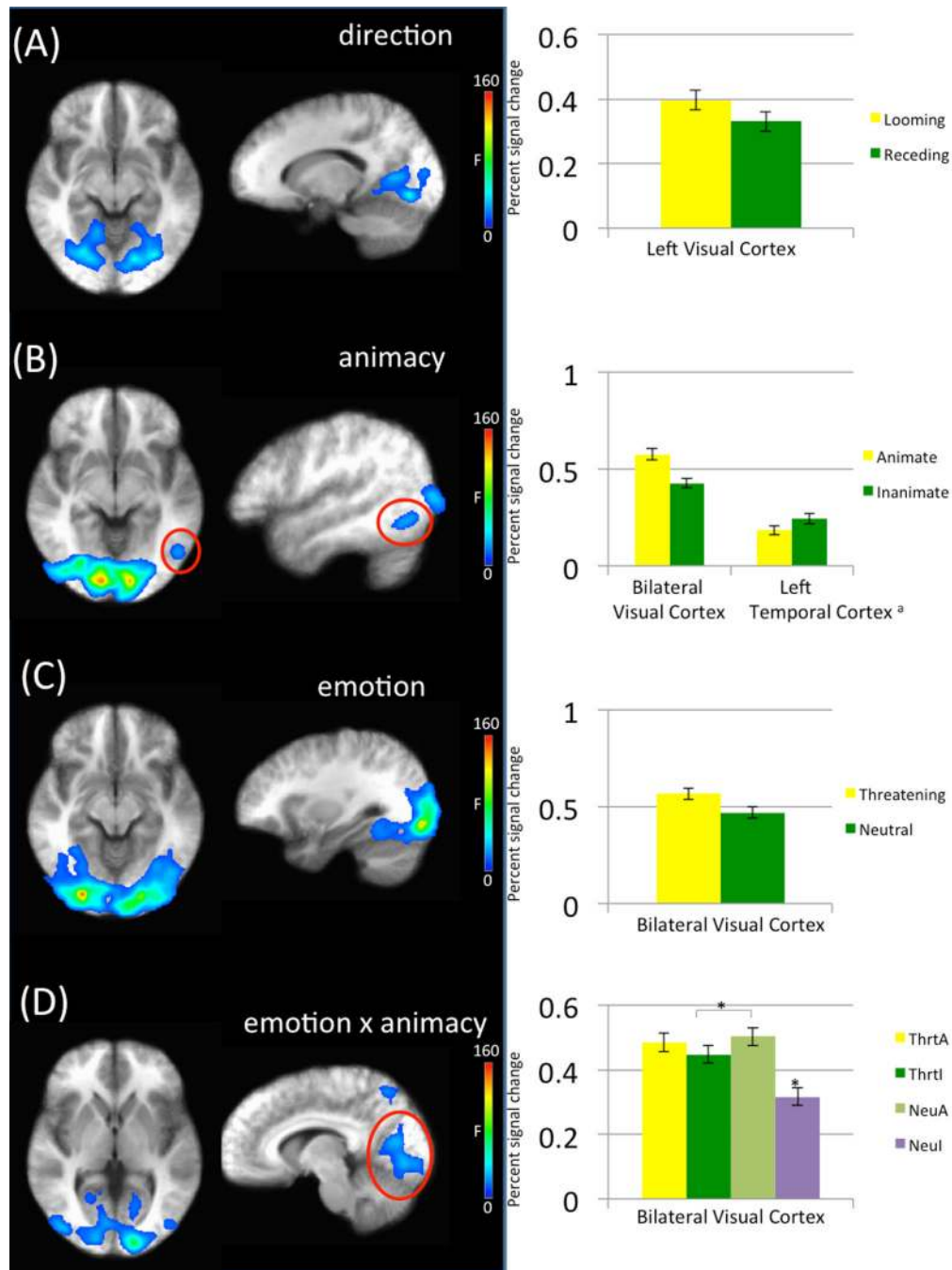**Figure 2.**
Significant amygdala responses to: (A) Emotion; (B) Animacy (a bilateral result with parameter estimates for both regions depicted); (C) Direction-by-Emotion; and (D) Direction-by-Animacy.
* = significant contrasts for interaction variables. Standard error bars depicted.

Figure 3.
Significant PAG responses to: (A) Emotion; and (B) Direction-by-Emotion.
Standard error bars depicted.

Figure 4.
Significant whole-brain responses to: (A) Direction; (B) Animacy; (C) Emotion; and (D) Emotion-by-Animacy Interaction.

ThrtA = Threatening Animate; ThrtI = Threatening Inanimate; NeuA = Neutral Animate; NeuI = Neutral Inanimate.

* = significant contrasts for interaction variables. Response to Neutral Inanimate variables is significantly less than response to all other conditions.

[a] = encircled region. Standard error bars depicted.

Table 1

Brain Regions Demonstrating Differential BOLD Responses During Task Performance in Regions of Interest

Contrast	Left/Right	BA	Coordinates of Peak Activation[a]			F (df=1,20)	p	Voxels
			x	y	z			
Amygdala								
Threatening > Neutral	Left		−22.5	−4.5	−15.5	6.35	.0188	2
Animate > Inanimate	Left		−18.5	−5.5	−11.5	8.94	.0064	5
Animate > Inanimate	Right		27.5	−5.5	−12.5	11.31	.0026	13
Looming > Recede	Left		−21.5	−5.5	−18.5	5.43	.0285	5
Looming > Recede	Right		26.5	−4.5	−21.5	9.52	.0051	7
Direction-by-Emotion Interaction	Left		−22.5	−8.5	−11.5	4.86	.0373	2
Direction-by-Animacy Interaction	Right		26.5	−4.5	−15.5	11.71	.0022	8
Periaqueductal Gray								
Threatening > Neutral	Right		3.5	−29.5	−1.5	15.99	.0005	10
Direction-by-Emotion Interaction	Right		7.5	−32.5	−7.5	11.56	.0024	3

[a]Based on the standard brain template of the Talairach & Tournoux Atlas. BA= Brodmann's Area, df= degrees of freedom

Table 2

Brain Regions Demonstrating Differential BOLD Responses During Task Performance

Region[a]	Left/Right	BA	Coordinates of Peak Activation[b]			F	p	Voxels
			x	y	z			
Emotion-by-Animacy								
precuneus	Right	7	7.5	−61.5	50.5	23.37	<.0001	69
occipital cortex	bilateral	17	−16.5	−88.5	5.5	90.90	<.0001	1820
Direction								
fusiform gyrus	Right	19	25.5	−64.5	−9.5	43.17	<.0001	712
fusiform gyrus	Left	18	−13.5	−70.5	−6.5	46.45	<.0001	613
Animacy								
middle temporal gyrus	Left	37	−49.5	−55.5	−9.5	36.28	<.0001	60
lingual gyrus	bilateral	17	−7.5	−88.5	2.5	225.7	<.0001	2910
Emotion								
occipital cortex	Right	18	25.5	−79.5	−9.5	163.2	<.0001	2762

[a] According to the Talairach Daemon Atlas (http://www.nitrc.org/projects/tal-daemon/).

[b] Based on the standard brain template of the Talairach & Tournoux Atlas. BA= Brodmann's Area