The human superior colliculus encodes looming- and object-related visual threat

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Abstract

The superior colliculus is an evolutionarily old midbrain structure involved in vision, attention, and motor control, enabling it to rapidly coordinate defensive responses to approaching threats. It remains unclear whether the human superior colliculus functions as a rudimentary threat detector, or if it uses highly processed information from cortex to facilitate threat processing. Here, we used convolutional neural networks and fMRI to characterize superior colliculus responses to naturalistic videos. We found that the human superior colliculus encoded visual looming and static object features, both of which were related to subjective fear ratings. Connectivity analyses revealed that looming and object-related signals in the superior colliculus covaried with a common network of regions including frontoparietal cortex, pulvinar, amygdala, and early visual, superior, and inferotemporal cortex. Object-related signals in the superior colliculus covaried more strongly with activity in the fusiform gyrus than looming-related signals, suggesting that static information about objects may reach the colliculus through cortical inputs. Together, these results characterize how the superior colliculus flexibly detects threats through its participation in distributed neural networks.

Keywords: neural encoding, vision, threat, superior colliculus, object, motion, fMRI, convolutional neural networks

Introduction

The superior colliculus is a midbrain structure involved in multiple functions—from object detection, visual attention, spatial reorienting, to coordinating defensive behavior (X. Liu et al., 2022). The mammalian superior colliculus is involved in the detection of looming objects (Cléry et al., 2020; Lee et al., 2020; Y.-J. Liu et al., 2011) and is necessary for active avoidance (Evans et al., 2018). Through its connectivity with diverse cortical systems, processing within the rodent superior colliculus is responsible for flexibly coordinating defensive behaviors, whether freezing or actively avoiding imminent threats (Li et al., 2023). At present, it is unclear whether similar computational principles apply to the human superior colliculus, or if superior colliculus activity is related to subjective emotional experience. Given evidence of object-selective responses in the primate superior colliculus (Yu et al., 2024) and dense projections to the superior colliculus from the ventral visual stream (Cerkevich et al., 2014; Fries, 1984), the human superior colliculus could use information about object category or looming motion to coordinate responses to threats. Here we evaluate these possibilities using task fMRI, naturalistic stimulation, and computational modeling with task-optimized artificial neural networks.

Methods

Naturalistic looming fMRI task. Healthy adult participants (*N* = 37 [sex: 32 F, 5 M; gender: 29 F, 5 M, 3 NB]; M_{age} = 27 yr, SD_{age} = 8 yr) viewed a series of naturalistic videos concurrent with 3T fMRI using a whole-brain MB8 sequence with 2.7 mm isotropic voxels. In an event related design, participants viewed a total of 91 video clips (mean duration = 7.76 sec, *SD* = 5.0 sec). Videos varied in terms of object type (dogs, cats, frogs, spiders, food dishes) and motion (the presence or absence of a looming object). After scanning, participants viewed the clips and reported valence, arousal, and fear for each item.

Encoding model specification and estimation. We trained voxel-wise encoding models to predict multivariate response patterns in the superior colliculus (defined anatomically using the Brainstem Navigator Atlas, García-Gomar et al., 2019). Visual features were defined using two task-optimized convolutional neural networks: a shallow convolutional network trained to detect imminent collision from patterns of optical flow (Zhou et al., 2022) that is known to predict human superior colliculus responses (Thieu et al., 2024) and a deep convolutional network for object recognition (AlexNet; Krizhevsky et al., 2012) that approximates transformations performed by the human ventral visual stream (Cichy et al., 2016; Eickenberg et al., 2017; Nonaka et al., 2021). We passed each video frame through the convolutional networks and extracted activations from the final layer of each network. Activations concatenated across the full duration of videos were used as predictors in multivariate encoding models to predict patterns of superior colliculus BOLD timeseries. Models were fit using partial least squares regression with 40 latent dimensions (to roughly equate model complexity). Generalization performance was estimated by computing the partial correlation between predicted and observed BOLD responses, adjusting for variance explained by the other model in a leave-one-subject-out cross-validation.

Covariation between superior colliculus responses, emotional experience, and large-scale brain networks. We tested whether superior colliculus responses were related to emotional experience by regressing self-report ratings on the average predicted superior colliculus response separately for looming- and object-related responses, estimating generalization using within subject split-half cross-validation. We estimated the separate contributions of looming- and object-related information by calculating the partial Spearman's ρ between observed ratings and looming-predicted and object-predicted ratings. Confidence intervals for these partial correlations were estimated via block bootstrapping, resampling observations grouped by subject.

We estimated the covariation between object- and looming- related activity in the superior colliculus and the rest of the brain. This was accomplished by calculating pairwise correlations between model-predicted superior colliculus time courses (averaged across superior colliculus voxels using data from held-out subjects) and the BOLD time course of all voxels in the brain. Inference on these maps was performed using group t-tests with a false discovery rate threshold of $q < .05$ (Benjamini & Hochberg, 1995).

Results

Superior colliculus responses encoded looming (mean cross-validated $r = .080$, 95% CI = [.068, .093]; Figure 1A) and object features (mean cross-validated $r = .120$, 95% CI = [.103, .136]). Direct comparisons revealed the two models explained unique variance in superior colliculus responses (looming features: partial $r = .027$, 95% CI = [.017, .037]; object features: partial $r = .107$, 95% CI = [.091, .123]). Object features explained a greater portion of variance than the looming model across superior colliculus voxels ($\Delta r = .039$, Cohen's $d = .86$). Multivariate decoding of encoding model responses showed that object stimulus categories could be classified both by object (5-way accuracy = 43.7%, $p_{\text{permuted}} < .001$) and looming features (accuracy = 37.0%, $p_{\text{permuted}} < .001$). Regressing self-report measures on looming- and object-related superior colliculus responses revealed that each variable was independently associated with self-report (Table 1).

Table 1. Partial correlations (95% CI) between self-report and superior colliculus responses

	Object Features	Looming Features
Valence	.238 [.192, .292]	.100 [.061, .138]
Arousal	.216 [.153, .301]	.086 [.026, .147]
Fear	.224 [.172, .277]	.116 [.061, .170]

Model-based connectivity analysis showed that representations of looming and object features in the superior colliculus covaried with BOLD signals in multiple regions (Figure 1B). Consistent with structural connectivity in nonhuman animals (X. Liu et al., 2022), we found common looming- and object-related functional connectivity with right inferior frontal gyrus, dorsal parietal cortex, pulvinar, amygdala, inferotemporal cortex, and lateral geniculate nucleus. Connectivity with inferotemporal cortex (predominantly in fusiform gyrus) was more strongly associated with superior colliculus signals related to object features compared to looming features.

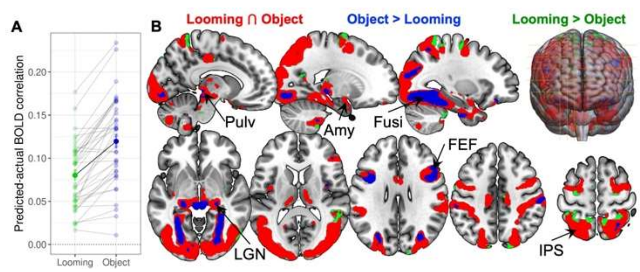

Figure 1. (A) Performance of superior colliculus encoding models estimated using leave-one-subject-out cross-validation. Each point corresponds to one subject; error bars reflect standard error of the mean. (B) Brain maps depicting the covariance between superior colliculus responses and BOLD responses.

Taken together, these results show that the superior colliculus encodes looming- and object-related information present in naturalistic videos, and that the superior colliculus participates in a distributed network of regions involved in detecting and responding to threats. These results are consistent with accounts suggesting that information from multiple cortical systems reaches the superior colliculus to flexibly yet rapidly coordinate behavior. More broadly, this work suggests the functional role of the superior colliculus may vary across species depending on the complexity of cortical contributions to midbrain processing.

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