Temporal asymmetries and interactions between dorsal and ventral visual pathways during object recognition

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Abstract

Despite their anatomical and functional distinctions, there is growing evidence that the dorsal and ventral visual pathways interact to support object recognition. However, the exact nature of these interactions remains poorly understood. Is the presence of identity-relevant object information in the dorsal pathway simply a byproduct of ventral input? Or, might the dorsal pathway be a source of input to the ventral pathway for object recognition? In the current study, we used high-density EEG – a technique with high temporal precision and spatial resolution sufficient to distinguish parietal and temporal lobes – to characterize the dynamics of dorsal and ventral pathways during object viewing. Using multivariate analyses, we found that category decoding in the dorsal pathway preceded that in the ventral pathway. Importantly, the dorsal pathway predicted the multivariate responses of the ventral pathway in a time-dependent manner, rather than the other way around. Together, these findings suggest that the dorsal pathway is a critical source of input to the ventral pathway.

Keywords: dorsal stream, ventral stream, object recognition, EEG, shape perception, multivariate analyses

Introduction

The primate visual system has historically been segregated into at least two independent visual pathways. The ventral visual pathway, which projects along the inferior temporal cortex (IT) and is involved primarily in visual object recognition, and the dorsal visual pathway, which projects along the parietal cortex and is involved primarily in visuospatial processing in the service of visually guided action. Despite their anatomical and functional differences, accumulating evidence suggests that the dorsal pathway may contribute to object recognition processes through its interactions with the ventral pathway. Yet, few studies have examined the precise temporal dynamics of object processing in dorsal and ventral pathways, leaving the directionality of these interactions unclear.

The dorsal pathway exhibits many functional properties that are crucial for object recognition. For instance, fMRI studies have shown that, like the ventral pathway, the dorsal pathway exhibited greater univariate activation to intact object images compared to scrambled object images, even when the objects did not afford action (Freud, Culham, et al., 2017; Grill-Spector et al., 1998). Moreover, the multivariate responses of dorsal regions were sufficient to decode an object's category across variations in the object's image-level properties and across variations among a category's exemplars (Bracci & Op de Beeck, 2016; Vaziri-Pashkam et al., 2019). Indeed, object classification accuracy in dorsal regions matched, and sometimes surpassed, classification accuracy of ventral object regions (Ayzenberg & Behrmann, 2022; Jeong & Xu, 2016). Other work has shown that applying transcranial magnetic stimulation (TMS) over the dorsal pathway impaired aspects of object perception, such as configural processing and global shape perception (Romei et al., 2011; Zachariou et al., 2017; Zaretskaya et al., 2013). And, indeed, many patient studies have shown that damage to the dorsal pathway may impair perception of global shape (Dalrymple et al., 2007; Karnath et al., 2000; Riddoch et al., 2008; Thomas et al., 2012). Thus, the dorsal pathway not only represents information crucial for action, but also represents identity-relevant object properties crucial for recognition.

There is also a high degree of anatomical and functional connectivity between dorsal and ventral pathways (Baizer et al., 1993; Kravitz et al., 2013; Takemura et al., 2016; Webster et al., 1994), suggesting that these pathways interact. However, the critical question regards the directionality of these interactions. Some studies have proposed that the ventral pathway transmits object information to the dorsal pathway to better specify the action affordances of objects (Almeida et al., 2013; Garcea & Mahon, 2014). Indeed, regions of the left parietal cortex (in right-handed participants) exhibited preferential functional connectivity with the ventral pathway when participants viewed images of tools – a category with a high-degree of affordance information. In this view, the dorsal pathway does not contribute to object recognition *per se* but represents identity-relevant object properties as a byproduct of ventral input.

An alternative proposal, however, is that the dorsal pathway computes identity-relevant properties independently of the ventral pathway and may even transmit object properties

to the ventral pathway to support recognition. Consistent with this proposal, intercranial recordings from a patient have revealed that object information can be decoded in the dorsal pathway prior to that in the ventral pathway (Regev et al., 2018). Moreover, temporary inactivation of the posterior parietal cortex (PPC) in monkeys reduces activation in ventral regions during object perception tasks (Van Dromme et al., 2016). Other research has shown that patients with extensive ventral damage nevertheless showed preserved responses to object shape in PPC, as well as an ability to recognize objects in certain contexts (Freud, Ganel, et al., 2017; Holler et al., 2019; Riddoch & Humphreys, 1987; Riddoch et al., 2008), suggesting that dorsal representations of shape are independent of the ventral pathway.

In a recent paper, Ayzenberg and Behrmann (2022) used fMRI to characterize the functional contributions of the dorsal pathway to the ventral pathway during object recognition. They found that object decoding performance in shape-selective regions of PPC was comparable to decoding performance in the lateral occipital cortex (LO) – a ventral region crucial for object recognition (Behrmann et al., 2016; Grill-Spector et al., 2001; Pitcher et al., 2009). Additionally, they found that the multivariate response of the dorsal pathway mediated representations of shape in the ventral pathway, with effective connectivity analyses revealing that PPC predicts the time course of LO activity, rather than the other way around. However, because fMRI has low temporal resolution, it is not possible to draw strong conclusions about the directionality of these interactions.

In the current study, we measure the temporal dynamics of the dorsal and ventral pathways using high-density electroencephalography (HD-EEG) – a neuroimaging method with millisecond precision and sufficient spatial resolution to localize dorsal and ventral pathways. Specifically, we selected channels of interest anatomically, corresponding to PPC and LO, and examined the directionality of their interactions. Although a limitation of EEG is its low spatial resolution, many studies have shown that the spatial resolution of HD-EEG is sufficient to dissociate lobes of the brain (Ferree et al., 2001; Hedrich et al., 2017). Indeed, concurrent fMRI and EEG recording have shown that HD-EEG can be used to localize retinotopic responses in visual cortex to within 8 mm of the fMRI responses (Im et al., 2007). Moreover, because PPC and LO are situated on the surface of the brain, recordings from these regions are less impacted by noise than is the case for deeper regions (Krishnaswamy et al., 2017). Thus, although the spatial resolution of HD-EEG is coarse when compared with other neuroimaging methods, it is sufficient to dissociate between neural activity in dorsal and ventral pathways.

We used an existing HD-EEG dataset in which participants were shown four categories of objects: tools, non-tools, insects, and birds (see Figure 1; Gurariy et al., 2022). In their initial study, Gurariy et al. (2022) used multivariate analyses and source localization to demonstrate comparable decoding of object shape, basic-level category, and category exemplar information in both dorsal and ventral pathways. However, they did not examine the temporal interactions between the pathways. Here, we characterized the object classification accuracy of each region across time and tested whether object category

information could be decoded earlier in dorsal or ventral areas. Moreover, we used Granger causality and time generalization analyses to examine whether the dorsal pathway predicted the time course of responses in the ventral pathway, or vice versa. To foreshadow our results, we found that object-related signals in the dorsal pathway preceded those of the ventral pathway, and that the dorsal pathway predicted the response of the ventral pathway in a time-dependent manner. Together, these findings suggest that the dorsal pathway is a critical source of input to the ventral pathway for object recognition.

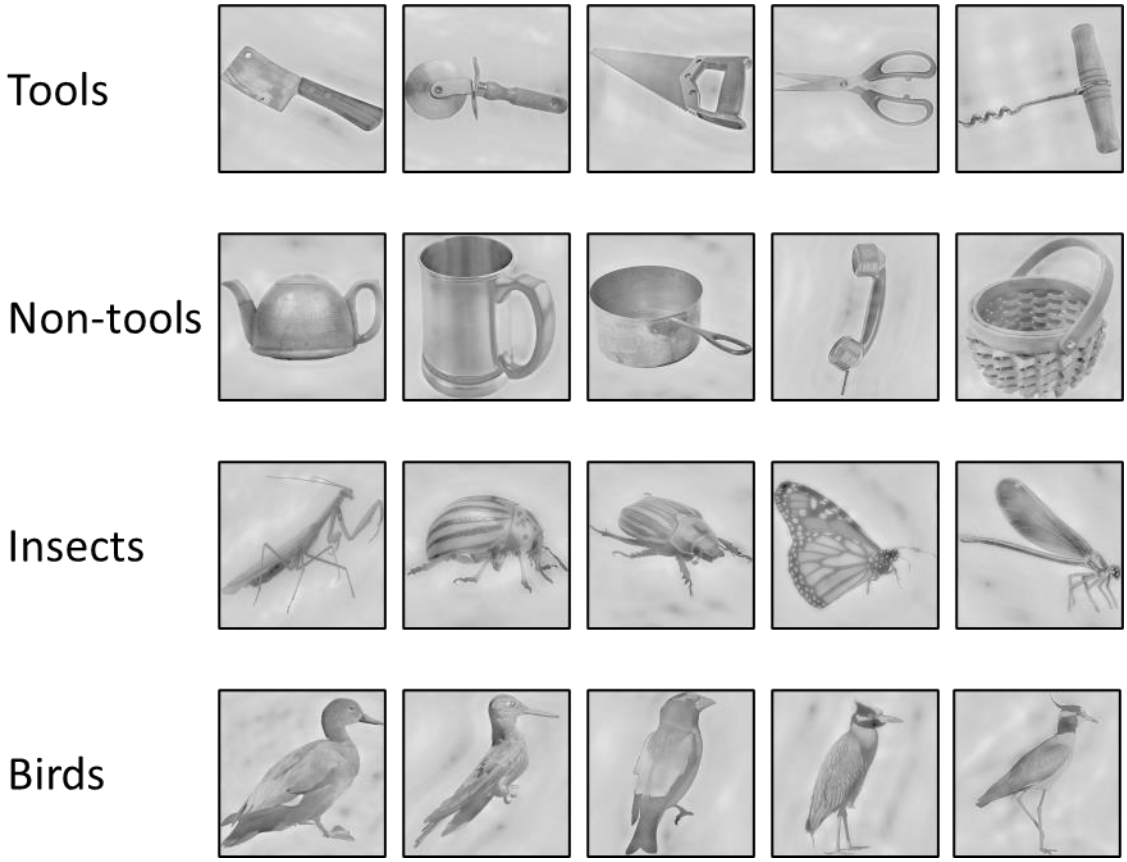

Figure 1. Stimuli presented to participants. Stimuli were comprised of four categories: tools, non-tools, insects, and birds. See Gurariy et al. (2022) for full details about stimulus design and presentation.

Methods

Participants

For a full description of the methods and procedures, see Gurariy et al. (2022). Twenty, right-handed, neurotypical adults (12 men, ages 18–38 years) with normal or corrected-to-normal visual acuity participated in the study. Each participant provided informed written consent. All protocols received approval by the institutional review board at the University of Nevada, Reno.

Apparatus

Stimuli were displayed on a Mitsubishi Diamond Pro270 CRT monitor (20 in., 1024 × 768) with a 120-Hz refresh rate, running via a 2.6-Mhz Mac Mini and presented using the PsychToolbox (Kleiner et al., 2007; Brainard, 1997; Pelli, 1997) for MATLAB (MathWorks Inc., 2007). Participants were seated 57 cm from the screen.

EEG Data Acquisition

The EEG signal was continuously recorded using a 256-channel HydroCel Geodesic Sensor Net via an EGI Net Amps Bio 300 amplifier (Electrical Geodesics Inc.) sampling at 1000 Hz. The digital data were recorded using Netstation 5.0(1) software. Impedance values were kept at or below 100Ω. A photodiode was used to validate frame-accurate timing of stimulus presentation.

EEG Preprocessing

EEG data were preprocessed using the EEG Lab Toolbox (Delorme & Makeig, 2004) and custom scripts written in MATLAB. Data were referenced from Cz to the algebraic average of all electrodes. A high bandpass of 0.1 Hz was applied to remove slow drift and electrical noise. Data were then down sampled from 1000 Hz to 250 Hz. Next, a low bandpass filter of 40 Hz was applied. Bad EEG channels were rejected using the 'pop_rejchan' and 'pop_clean_rawdata' functions in EEG Lab by identifying channels with extended flat line recordings and minimal channel correlation using joint probability of the recorded electrode. Independent component analysis (ICA) was used to identify and remove residual blink artifacts. Across participants, an average of 15.2 % of channels were removed.

The filtered time series was then segmented into 550-msec epochs (a 50-msec pre-stimulus baseline followed by 500 msec of electrophysiological data after stimulus onset). Event segmentation was performed using trigger markers that were sent to the acquisition computer at the onset of each trial. The temporal offset that existed between the physical presentation of the stimulus and the registration of the stimulus marker in the acquisition computer was measured using a photodiode and corrected for during trial segmentation. Following event segmentation, artifacts were detected using EEG Lab functions (pop_eegthresh) which rejects artifacts using thresholding. The EEG epochs described above for each participant were grouped into four conditions: tools, non-tools, insects, and birds.

Channel Selection

Anatomically defined channels of interest were selected a priori in regions corresponding to PPC and LO using a cortical projection of EEG sensors (Koessler et al., 2009; Luu & Ferree, 2005). Specifically, channels were identified by first overlaying a PPC (IPS0 and IPS1; Wang et al., 2014) and LO (Julian et al., 2012) probabilistic masks on a standard MNI brain with the Juliech Atlas, and determining the corresponding Brodmann areas for each (see Figure 2A). Channels corresponding to PPC (BA 7 and superior 19) and LO (BA 18 and inferior 19) were then identified using a template brain with electrodes arranged in the 10-10 system (Koessler et al., 2009). PPC electrodes consisted of 14 channels in the left hemisphere located approximately between P3 and Pz locations and 14 channels in the right hemisphere located approximately between Pz and P4 locations (see Figure 2B). LO electrodes consisted of 14 channels in the left hemisphere located approximately between the T5 and O1 locations, and 14 channels in the right hemisphere located approximately between T6 and O2 locations (see Figure 2B).

To further validate our channel selection decisions, we tested whether our anatomically defined dorsal and ventral channels could also be distinguished functionally. Principal component analysis (PCA) was conducted on all channels for each participant, and we retained components that explained 95 % of the variance. Then, we tested whether dorsal and ventral channels load onto similar components, respectively. Specifically, calculated the Euclidean distance between the component loadings for each channel with every other channel in a pairwise fashion, providing a metric of functional similarity between all channels. Hierarchical cluster analyses of the mean participant similarity matrix revealed that our anatomically selected dorsal channels are more similar to one another than ventral channels, and vice versa for ventral channels (Figure 2C).

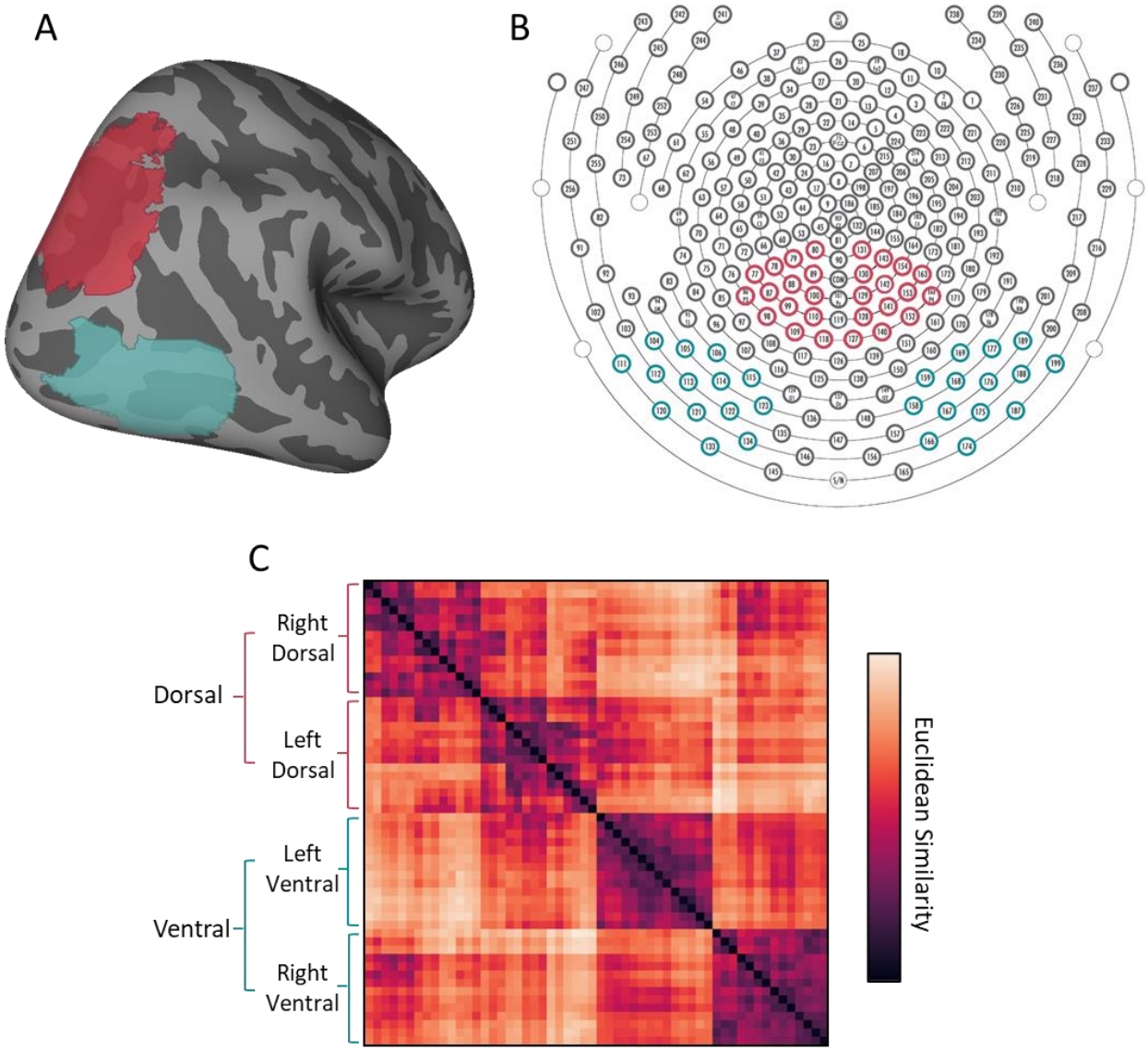

Figure 2. Anatomical regions of interest and their corresponding HD-EEG channels. (A) Probabilistic parcels for (red) PPC and (blue) LO projected onto an inflated standard brain (right hemisphere). (B) A diagram illustrating the channels of interest corresponding anatomically to (red) PPC and (blue) LO. (C) A cluster map illustrating the similarity between dorsal and ventral EEG channels. Hierarchical clustering of EEG channels revealed that dorsal channels were functionally more similar to one another than to ventral channels; likewise, ventral channels were functionally more similar to one another than to dorsal channels.

Stimuli and procedure

The stimuli comprised four categories (tools, non-tools, birds, insects), each consisting of five exemplars (resulting in 20 unique images; see Figure 1). All stimuli were processed using the SHINE toolbox (Willenbockel et al., 2010) to control for low-level differences in luminance and spatial frequency.

On each trial, an image was presented at the center of the screen (15° × 15°) for 300 msec followed by an interstimulus interval (ISI) lasting between 800 and 1200 msec. Each of the 20 exemplars that made up the four categories was presented 84 times resulting in 420 trials per condition and 1680 trials in total. The order of presentation was randomized. To maintain their attention, participants performed an orthogonal task wherein they pressed the space bar if an image appeared at a reduced luminance (50%), and this occurred on 5% of the trials. Reduced luminance trials were excluded from all subsequent analysis.

Data analysis

Event-related potentials. For each participant and region, the event-related potential (ERP) waveform for every object was averaged together, and their absolute value taken. The ERP signal was then normalized by subtracting the response at every timepoint from the mean response during the pre-stimulus period (-50 ms to 0 ms). Above baseline (i.e., greater than 0) response at each timepoint was determined using a bootstrap procedure, wherein participants' ERP data was resampled 10,000 times (with replacement) and 95% bootstrap confidence intervals were constructed around the response for each timepoint. Qualitatively similar results were found using different analysis methods (e.g., one-sample t-test comparisons to chance).

Category decoding. For each participant, region and timepoint, a support vector machine (SVM) classifier was trained on the multivariate pattern for three exemplars from each category, and then required to predict the category of the two left out exemplars (20-fold cross-validation). Above chance (0.25) decoding accuracy for each timepoint was determined using a bootstrap procedure, wherein participants' decoding data was resampled 10,000 times (with replacement) and 95% bootstrap confidence intervals were constructed around the classification accuracy for each timepoint. Qualitatively similar results were found when using different classifiers (e.g., Naïve bayes) or statistical tests (e.g., one-sample t-test comparisons to chance).

Effective connectivity. For each participant and region, the channel × time (stimulus onset to offset) response for each object was concatenated to one another to form one continuous timeseries. A single null value was inserted between every object's timeseries to prevent prediction of temporally discontinuous timepoints. Multivariate Granger causality analyses (Barnett & Seth, 2014; Barrett et al., 2010) were then conducted twice, once with the dorsal pathway channels as the predictor and once with the ventral pathway channels as the predictor. Following prior work (Roebroeck et al., 2005), effective connectivity between the areas was calculated by subtracting the dorsal → ventral F statistic from the ventral → dorsal F statistic. Multivariate Granger causality was tested with a maximum lag of 50 ms, with the best fitting lag for each direction used to compare dorsal and ventral pathways. Following previous work, a group analysis was conducted using a Wilcoxon signed-rank test comparing F-difference values to 0.

Time generalized representational similarity analyses. For each participant and region, a 20 × 20 representational dissimilarity matrix (RDM) was created for every time point by

computing the Cosine similarity between the multivariate channel responses for one object with every other object in a pairwise fashion. RDMs were then averaged across participants separately for PPC and LO. Then, for every timepoint, the upper triangle of the resulting matrix (including the diagonal) for the dorsal pathway was correlated with the RDM of every timepoint of ventral pathway. To test whether the dorsal pathway predicted the ventral pathway, or the other way around, we subtracted the correlations below the diagonal (dorsal → ventral) from the correlations above the diagonal (ventral → dorsal). Specifically, for each participant, we subtracted each timepoint from the timepoint with the equivalent coordinates mirrored along the diagonal. For example, the timepoint with coordinates 100 ms in the dorsal pathway (*y*-axis) and 120 ms in the ventral pathway (*x*-axis) was subtracted from the time point with coordinates 120 ms in the ventral pathway and 100 ms in the dorsal pathway. A significant positive difference from 0 would indicate that the dorsal pathway better predicts future times points of the ventral pathway, rather than the other way around. The mean difference across all correlation subtractions was taken for each participant, and submitted to a one-sample t-test comparison to chance (0).

Results

Onset of visual information in dorsal and ventral pathways

We first used ERP analyses to determine the time point at which a stimulus was identifiable from the EEG signal (see Figure 3). We found that object-evoked responses reach their peak earlier in the dorsal (230 ms) than the ventral pathway (250 ms). Moreover, we found that ERP signal was first above chance in the dorsal pathway at 26 ms, whereas ERPs were first above chance in the ventral pathway at 42 ms, a difference of 16 ms (see Figure 3A).

Next, we tested whether these timing differences between dorsal and ventral pathways were statistically consistent. Participant data from dorsal and ventral pathways was resampled 1,000 times (with replacement). On each resample, a one-sided, one-sample t-test was conducted for every timepoint of participants' data, and the first timepoint with above chance response was recorded. To minimize spurious significant timepoints, only those timepoints with an above chance response for at least two consecutive timepoints were recorded (results were qualitatively similar without this step).

Across resamples of the data, the response in the dorsal pathway was on average 10.47 ms earlier than in the ventral pathway. A Binomial comparison to chance (0.50) revealed that the dorsal pathway preceded the ventral pathway in 59.6% of resamples, significantly more often than would be predicted by chance (0.50; $p < 0.001$; Binomial test; see Figure 3B). These results provide initial evidence that object information may be present in the dorsal pathway prior to the ventral pathway.

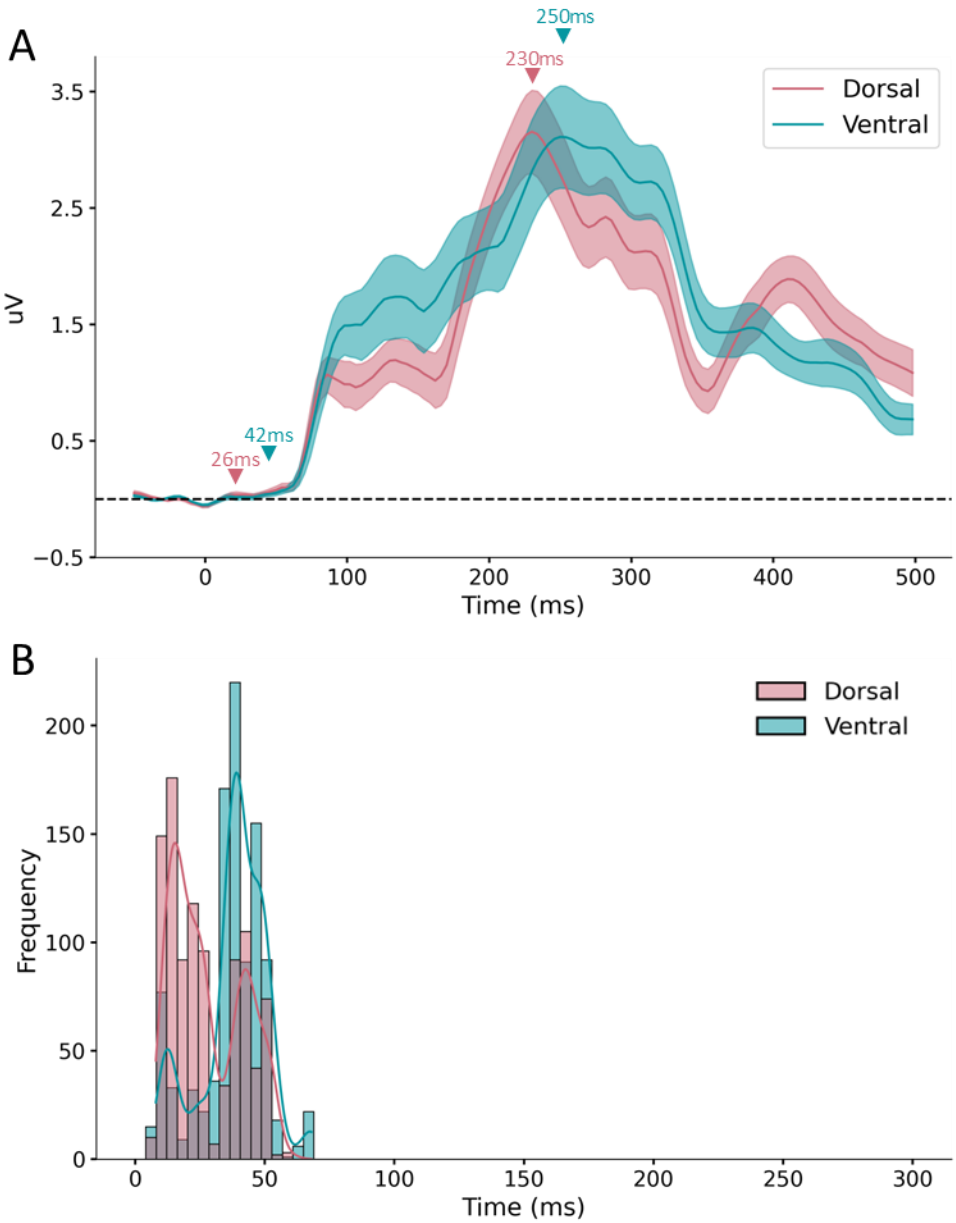

Figure 3. Results of the ERP analyses. (A) ERP waveform for (red) dorsal and (blue) ventral channels. Responses are plotted along the y-axis as a function of time (ms). Data are plotted from the pre-stimulus period to post-stimulus period (-50 ms to 500 ms). Shaded regions indicate standard error of the mean (SE). (B) A histogram illustrating the earliest onset of an above chance response for 1,000 resamples for (red) dorsal and (blue) ventral channels. The y-axis illustrates frequency with which each time point exhibited an above chance response. Data are plotted for the stimulus period (0 ms to 300 ms).

The time course of object classification

Although the analysis above suggests that object information may be present in the dorsal pathway prior to the ventral pathway, it is not clear whether this information is relevant for object recognition. Indeed, the early visual response of the dorsal pathway may be for the purpose of action, rather than recognition. Thus, in the next analysis we examine the time course of identity-relevant object information in the dorsal and ventral pathways. Specifically, we tested when the multivariate pattern in each area could be used to decode the objects' categories (see Figure 4).

We found that peak decoding accuracy was comparable in both pathways, with the peak accuracy at 210 ms in the dorsal pathway (34.8%) and 214 ms in ventral pathways (35.8 %). But the critical question has to with the temporal signature, namely, in which cortical area was object information decoded earlier in time? An analysis of the first onset of significant decoding found that object category information could be decoded above chance earlier from the dorsal pathway (28.3 %) at 66 ms, whereas category information was decoded from the ventral pathway (29.1%) at 82 ms, a difference of 16 ms (see Figure 4A).

We next tested whether these timing differences between dorsal and ventral pathways were statistically consistent. As above, participant data from dorsal and ventral pathways was resampled 1,000 times (with replacement). On each resample a one-sided, one-sample t-test was conducted for every timepoint of participants' data, and the first timepoint with above chance decoding was recorded. Again, to minimize spuriously significant timepoints, only those timepoints with significant decoding for at least two consecutive timepoints were recorded (results were qualitatively similar without this step).

Across resamples of the data, the decoding in the dorsal pathway was on average 15.95 ms earlier than in the ventral pathway. A Binomial comparison to chance (0.50) revealed that the dorsal pathway preceded the ventral pathway in 66.9% of resamples, significantly more often than would be predicted by chance (0.50; $p < 0.001$; Binomial test; see Figure 4B). Altogether, these results show that identity-relevant object information is present in the dorsal pathway prior to the ventral pathway.

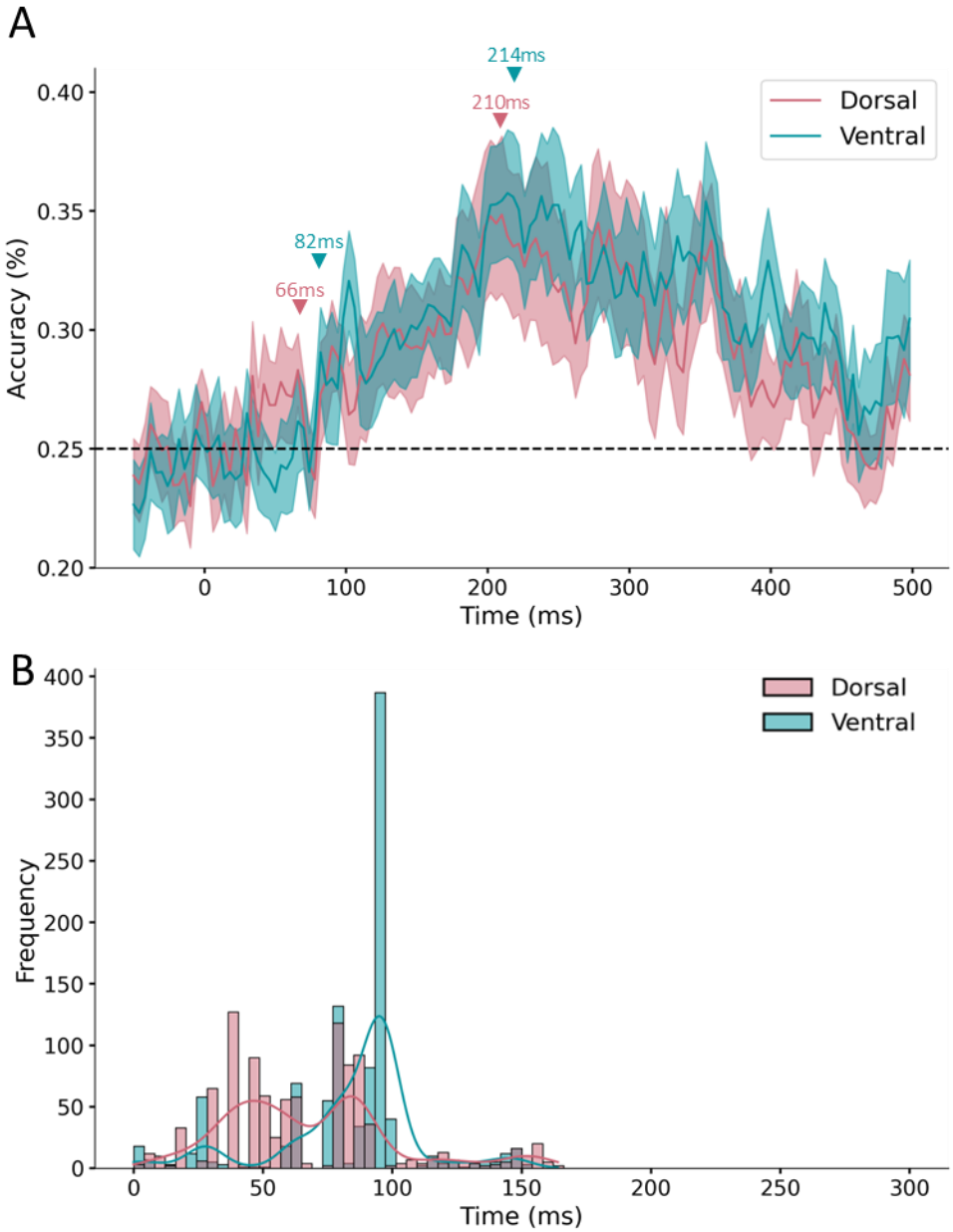

Figure 4. Results of the decoding analyses. (A) Time course of category decoding for (red) dorsal and (blue) ventral channels. Classification accuracy is plotted along the y-axis as a function of time (ms). Data are plotted from the pre-stimulus period to post-stimulus period (-50 ms to 500 ms). Shaded regions indicate standard error of the mean (SE). (B) A histogram illustrating the earliest onset of above chance classification for 1000 resamples for (red) dorsal and (blue) ventral channels. The y-axis illustrates proportion with which each time point exhibited above chance classification accuracy. Data are plotted for the stimulus period (0 ms to 300 ms).

Effective connectivity analyses

The results above revealed that object classification in the dorsal pathway preceded that of the ventral pathway. However, it is unclear whether the dorsal pathway is also a source of input to the ventral pathway. Indeed, it is possible that object processing simply occurs in parallel in dorsal and ventral pathways with a temporal advantage for dorsal over ventral but with little, if any, interaction.

To test whether the dorsal pathway is a potential source of input to the ventral pathway, we conducted hypothesis-driven multivariate Granger causality analyses (Barnett & Seth, 2014; Barrett et al., 2010). The premise underlying Granger causality analyses is as follows. The dorsal pathway can be said to predict the response of ventral pathway if incorporating the past multivariate responses of dorsal pathway (i.e., *t*-1) improves the prediction of current multivariate responses of the ventral pathway over above ventral's own past responses.

Granger causality analyses were conducted in both directions (dorsal → ventral and ventral → dorsal), with the resulting *F* statistics subtracted from one another. A Wilcoxon signed-rank one-sample *t*- tests comparisons to 0 revealed significant effective connectivity from the dorsal to the ventral pathway, $W(19) = 172$, $p = .011$, $d = 0.64$. This finding suggests that the multivariate time course of the dorsal pathway predicts the ventral pathway, rather than the other way around.

Time generalization analyses

If the dorsal pathway precedes and predicts future responses of the ventral pathway, then the strongest correlation between dorsal and ventral pathways should be between the present time point of the dorsal pathway with future timepoints of the ventral pathway. To test this prediction, we conducted time generalized representational similarity analyses (King & Dehaene, 2014; Kriegeskorte et al., 2008).

See Figure 5A for the time generalization matrix. Across participants, correlations were stronger when the dorsal pathway was correlated with future timepoints of the ventral pathway, than when the ventral pathway was correlated with future timepoints of the dorsal pathway, $t(19) = 2.22$, $p = .039$, $d = 0.49$.

To further visualize the patterns of interactions between dorsal and ventral pathways, we rank ordered the correlations from strongest to weakest and labeled each according to whether they reflected dorsal → ventral correlations, ventral → dorsal correlations, or correlations along the diagonal of the matrix (see Figure 5B). This visualization revealed that the strongest correlations were overwhelmingly those where dorsal signals predicted ventral signals. Indeed, 9 of the 10 strongest correlations are those in which the dorsal pathway predicted ventral pathway, with the single remaining value reflecting a correlation along the diagonal of the matrix. The mean prediction delay between dorsal and ventral pathways was 8.8 ms.

To characterize this pattern quantitatively, we conducted a rolling Binomial analysis in increments of 50, where we tested whether dorsal → ventral correlations comprise a larger proportion of the correlations than would be predicted by chance (0.49). This analysis revealed that dorsal → ventral correlations comprised the majority of the top correlations up to the first 500 indexed correlations (55.2%, $p = 0.006$). At its peak, dorsal → ventral correlations comprised 66% of the top 300 correlations ($p < 0.001$), with a mean prediction delay of 34.3 ms. Altogether these results suggest that the dorsal pathway predicts the future response of the ventral pathway, rather than other way around.

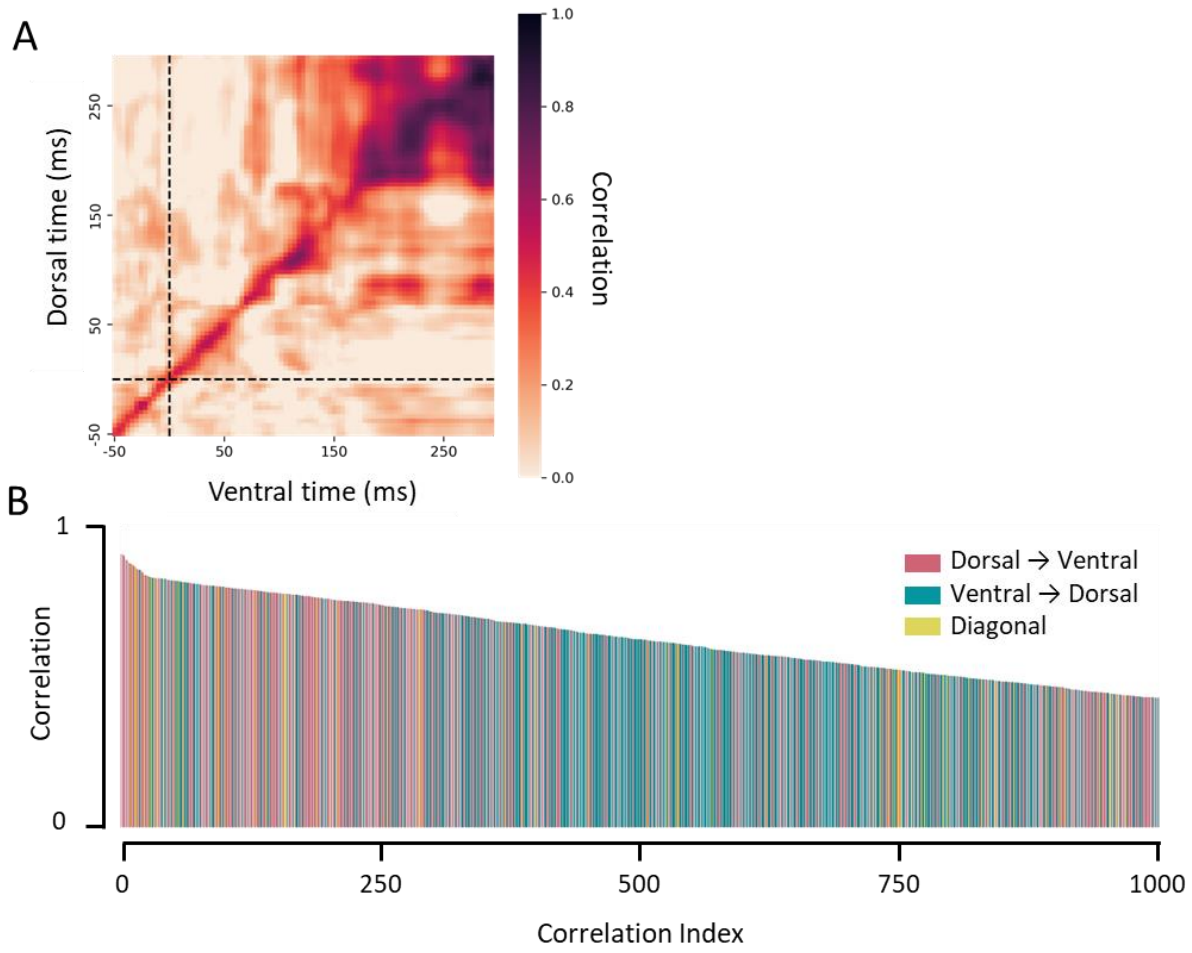

Figure 5. Time generalized representational similarity analyses. (A) Time generalization matrix illustrating the correlation between RDMs for each dorsal time point with each ventral time point. Correlations were stronger for dorsal → ventral correlations than ventral → dorsal correlations. Data are plotted from the pre-stimulus to stimulus offset period (-50 ms to 300 ms). Dotted line indicates stimulus onset. (B) Top 1000 correlations, rank ordered from highest to lowest for (red) dorsal → ventral correlations, (blue) ventral → dorsal correlations, and (yellow) correlations along the time diagnol.

General Discussion

In the current study, we examined the temporal dynamics and interactions of the dorsal and ventral visual pathways and their respective contributions to object perception. Although an increasing number of studies have proposed that dorsal and ventral pathways interact during the process of object recognition, few studies have examined the timing and directionality of object processing in the two visual pathways. Using HD-EEG, we found that the dorsal pathway represented identity-relevant object information prior to the ventral pathway. Moreover, we found that the dorsal pathway predicted the response of the ventral pathway in a time-dependent manner. Altogether, these findings suggest that identity-relevant object information in the dorsal pathway arises independently of the ventral pathway, and may be a source of input to the ventral pathway for object recognition.

However, a limitation of the current study is that EEG and the study design affords only coarse anatomical specificity. Although previous work has shown that HD-EEG can localize visual responses to within 8 mm of their anatomical location (Im et al., 2007), the precise anatomical location of our channels of interest is not clear. Specifically, we used a standard brain template to select channels that encompass PPC and LO. However, it is possible that our channel selection also included signals from adjacent regions and potentially reduced the strength of the results. Indeed, the diffuse nature of the EEG signal essentially guarantees that our measurements were influenced by responses from areas outside our regions of interest. Nevertheless, HD-EEG does have sufficient spatial resolution to dissociate lobes of the brain (Ferree et al., 2001; Hedrich et al., 2017), allowing us to generally distinguish between dorsal and ventral pathways. Moreover, PCA of the EEG channels revealed that our anatomically-selected dorsal and ventral channels load on similar components for each region, respectively. It is also important to note that, the spatial limitations of HD-EEG should have attenuated any timing differences between dorsal and ventral pathways, not strengthened them. That we consistently found that the dorsal pathway precedes and predicts the ventral pathway across a range of analyses suggests that our results are based on signals from distinct regions. Indeed, it is likely that our results underestimate the true temporal asymmetries and interactions between dorsal and ventral pathways. Nevertheless, future work using intracranial recording with patients (Regev et al., 2018), or concurrent scalp EEG and MRI recordings will be needed to strengthen these conclusions.

Our results are most consistent with the dorsal pathway as a source of input to the ventral pathway. However, it is almost certainly the case that there are bidirectional interactions between the two pathways (Kravitz et al., 2011; Kravitz et al., 2013). For instance, at later stages of processing, the ventral pathway may provide concept-level information about an object's affordances to the dorsal pathway to help coordinate actions (Almeida et al., 2013; Garcea & Mahon, 2014). Moreover, identity-relevant object information may be transmitted in a recurrent manner between dorsal and ventral pathways as needed to accomplish object recognition. Such recurrent interactions may be particularly important

in challenging contexts where objects properties are difficult to identify (Bar et al., 2006; Kar et al., 2019; Tang et al., 2018). Nevertheless, our findings suggest that, in the early stages of object processing, the dorsal pathway is an initial source of input to the ventral pathway, a finding consistent with existing intracranial recording work with a patient (Regev et al., 2018). Future work should examine how the directionality and dynamics of dorsal-ventral interactions change for different tasks and anatomical stages.

However, a crucial question is, what kind of information does the dorsal pathway actually transmit to the ventral pathway for object recognition? The first possibility is that the dorsal pathway transmits depth information to the ventral pathway, supporting the perception of 3D shape (Freud et al., 2020; Orban, 2011; Welchman, 2016). Many studies have shown that the dorsal pathway is crucial for perceiving depth information, with the PPC responding more strongly to 3D objects (e.g., as defined by disparity or texture) than 2D shapes (Georgieva et al., 2009; Georgieva et al., 2008; Liu et al., 2004). Moreover, inactivation of PPC from stimulation or damage impairs the perception of an object's depth structure (Chang et al., 2014; Chowdhury & DeAngelis, 2008; Gillebert et al., 2015; Van Dromme et al., 2016). Thus, the dorsal pathway may compute the depth structure of objects to better support object recognition across viewpoints (Farivar, 2009; Humphrey & Jolicoeur, 1993; Oliver et al., 2018).

Another possibility is that that the dorsal pathway plays a critical role in computing an object's structural description and transmits this information to the ventral pathway for recognition (Romei et al., 2011; Zachariou et al., 2017; Zaretskaya et al., 2013). Structural descriptions are a representation of 'global shape', which describe the spatial relations between an object's parts, without describing the appearance of the parts themselves (Barenholtz & Tarr, 2006; Biederman, 1987; Hummel, 2000). Such a description is crucial for invariant object recognition as the object's structure stays relatively stable across variations in viewpoint (Ayzenberg et al., 2019; Biederman, 2000; Biederman & Bar, 1999). Structural descriptions may also be central to basic-level categorization as exemplars within a category share the same structure, while varying in their individual features (Ayzenberg & Lourenco, 2022; Ayzenberg & Lourenco, 2019; Rosch et al., 2004; Tarr & Bülthoff, 1995). The dorsal pathway may be ideally suited to compute such a representation given its well-known role in computing spatial relations more generally. Indeed, recent studies have found regions in PPC that were functionally selective for an object's structure, independent of other properties represented by the dorsal pathway, such as depth (Ayzenberg & Behrmann, 2022). These PPC regions were capable of decoding an object's category and mediated representations of structure in the ventral pathway (Ayzenberg et al., 2022). Thus, not only might the dorsal pathway compute the spatial relations between objects to support action, but it may also compute the relations between object parts so as to form more complete representations of shape, in conjunction with ventral pathway.

In summary, our results expand our understanding of the interactions between dorsal and ventral visual pathways. Although it is increasingly accepted that the two visual pathways

interact, the precise nature of these interactions remained poorly understood. Here we showed that identity-relevant object processing in the dorsal pathway precedes and predicts processing in the ventral pathway. Together, these findings provide an expanded understanding of how object processing unfolds in the visual system.

References

Almeida, J., Fintzi, A. R., & Mahon, B. Z. (2013). Tool manipulation knowledge is retrieved by way of the ventral visual object processing pathway. *Cortex, 49*(9), 2334-2344. doi:https://doi.org/10.1016/j.cortex.2013.05.004

Ayzenberg, V., & Behrmann, M. (2022). The dorsal visual pathway represents object-centered spatial relations for object recognition. *Journal of Neuroscience*.

Ayzenberg, V., Chen, Y., Yousif, S. R., & Lourenco, S. F. (2019). Skeletal representations of shape in human vision: Evidence for a pruned medial axis model. *Journal of Vision, 19*(6), 1-21. doi:10.1167/19.6.6

Ayzenberg, V., Kamps, F. S., Dilks, D. D., & Lourenco, S. F. (2022). Skeletal representations of shape in the human visual cortex. *Neuropsychologia*, 108092. doi:10.1016/j.neuropsychologia.2021.108092

Ayzenberg, V., & Lourenco, S. (2022). Perception of an object's global shape is best described by a model of skeletal structure in human infants. *eLife, 11*, e74943. doi:10.7554/eLife.74943

Ayzenberg, V., & Lourenco, S. F. (2019). Skeletal descriptions of shape provide unique perceptual information for object recognition. *Scientific Reports, 9*(1), 1-13. doi:10.1038/s41598-019-45268-y

Baizer, J. S., Desimone, R., & Ungerleider, L. G. (1993). Comparison of subcortical connections of inferior temporal and posterior parietal cortex in monkeys. *Visual Neuroscience, 10*(1), 59-72.

Bar, M., Kassam, K. S., Ghuman, A. S., Boshyan, J., Schmid, A. M., Dale, A. M., . . . Halgren, E. (2006). Top-down facilitation of visual recognition. *Proceedings of the National Academy of Sciences of the United States of America, 103*(2), 449-454. doi:10.1073/pnas.0507062103

Barenholtz, E., & Tarr, M. J. (2006). Reconsidering the Role of Structure in Vision. In *Psychology of learning and motivation* (Vol. 47, pp. 157-180): Academic Press.

Barnett, L., & Seth, A. K. (2014). The MVGC multivariate Granger causality toolbox: a new approach to Granger-causal inference. *Journal of neuroscience methods, 223*, 50-68.

Barrett, A. B., Barnett, L., & Seth, A. K. (2010). Multivariate Granger causality and generalized variance. *Physical Review E, 81*(4), 041907.

Behrmann, M., Lee, A. C. H., Geskin, J. Z., Graham, K. S., & Barense, M. D. (2016). Temporal lobe contribution to perceptual function: A tale of three patient groups. *Neuropsychologia, 90*, 33-45. doi:https://doi.org/10.1016/j.neuropsychologia.2016.05.002

Biederman, I. (1987). Recognition-by-components: a theory of human image understanding. *Psychological Review, 94*(2), 115-147.

Biederman, I. (2000). Recognizing depth-rotated objects: A review of recent research and theory. *Spatial Vision, 13*(2), 241-253.

Biederman, I., & Bar, M. (1999). One-shot viewpoint invariance in matching novel objects. *Vision Research, 39*(17), 2885-2899.

Bracci, S., & Op de Beeck, H. (2016). Dissociations and associations between shape and category representations in the two visual pathways. *Journal of Neuroscience, 36*(2), 432-444.

Chang, Dorita H. F., Mevorach, C., Kourtzi, Z., & Welchman, Andrew E. (2014). Training Transfers the Limits on Perception from Parietal to Ventral Cortex. *Current Biology, 24*(20), 2445-2450. doi:https://doi.org/10.1016/j.cub.2014.08.058

Chowdhury, S. A., & DeAngelis, G. C. (2008). Fine discrimination training alters the causal contribution of macaque area MT to depth perception. *Neuron, 60*(2), 367-377.

Dalrymple, K. A., Kingstone, A., & Barton, J. J. (2007). Seeing trees OR seeing forests in simultanagnosia: attentional capture can be local or global. *Neuropsychologia, 45*(4), 871-875.

Delorme, A., & Makeig, S. (2004). EEGLAB: an open source toolbox for analysis of single-trial EEG dynamics including independent component analysis. *Journal of neuroscience methods, 134*(1), 9-21.

Farivar, R. (2009). Dorsal–ventral integration in object recognition. *Brain research reviews, 61*(2), 144-153.

Ferree, T. C., Clay, M. T., & Tucker, D. M. (2001). The spatial resolution of scalp EEG. *Neurocomputing, 38-40*, 1209-1216. doi:https://doi.org/10.1016/S0925-2312(01)00568-9

Freud, E., Behrmann, M., & Snow, J. C. (2020). What does dorsal cortex contribute to perception? *Open Mind, 4*, 40-56.

Freud, E., Culham, J. C., Plaut, D. C., & Behrmann, M. (2017). The large-scale organization of shape processing in the ventral and dorsal pathways. *eLife, 6*, e27576.

Freud, E., Ganel, T., Shelef, I., Hammer, M. D., Avidan, G., & Behrmann, M. (2017). Three-dimensional representations of objects in dorsal cortex are dissociable from those in ventral cortex. *Cerebral Cortex, 27*(1), 422-434.

Garcea, F. E., & Mahon, B. Z. (2014). Parcellation of left parietal tool representations by functional connectivity. *Neuropsychologia, 60*, 131-143. doi:https://doi.org/10.1016/j.neuropsychologia.2014.05.018

Georgieva, S., Peeters, R., Kolster, H., Todd, J. T., & Orban, G. A. (2009). The Processing of Three-Dimensional Shape from Disparity in the Human Brain. *The Journal of Neuroscience, 29*(3), 727-742. doi:10.1523/jneurosci.4753-08.2009

Georgieva, S. S., Todd, J. T., Peeters, R., & Orban, G. A. (2008). The Extraction of 3D Shape from Texture and Shading in the Human Brain. *Cerebral Cortex, 18*(10), 2416-2438. doi:10.1093/cercor/bhn002

Gillebert, C. R., Schaeverbeke, J., Bastin, C., Neyens, V., Bruffaerts, R., De Weer, A.-S., . . . Vandenberghe, R. (2015). 3D Shape Perception in Posterior Cortical Atrophy: A Visual Neuroscience Perspective. *The Journal of Neuroscience, 35*(37), 12673-12692. doi:10.1523/jneurosci.3651-14.2015

Grill-Spector, K., Kourtzi, Z., & Kanwisher, N. (2001). The lateral occipital complex and its role in object recognition. *Vision Research, 41*(10), 1409-1422.

Grill-Spector, K., Kushnir, T., Hendler, T., Edelman, S., Itzchak, Y., & Malach, R. (1998). A sequence of object-processing stages revealed by fMRI in the human occipital lobe. *Human Brain Mapping, 6*(4), 316-328.

Gurariy, G., Mruczek, R. E., Snow, J. C., & Caplovitz, G. P. (2022). Using High-Density Electroencephalography to Explore Spatiotemporal Representations of Object Categories in Visual Cortex. *Journal of Cognitive Neuroscience, 34*(6), 967-987.

Hedrich, T., Pellegrino, G., Kobayashi, E., Lina, J. M., & Grova, C. (2017). Comparison of the spatial resolution of source imaging techniques in high-density EEG and MEG. *Neuroimage, 157*, 531-544. doi:https://doi.org/10.1016/j.neuroimage.2017.06.022

Holler, D. E., Behrmann, M., & Snow, J. C. (2019). Real-world size coding of solid objects, but not 2-D or 3-D images, in visual agnosia patients with bilateral ventral lesions. *Cortex, 119*, 555-568. doi:https://doi.org/10.1016/j.cortex.2019.02.030

Hummel, J. E. (2000). Where view-based theories break down: The role of structure in shape perception and object recognition. In E. Dietrich & A. Markman (Eds.), *Cognitive dynamics: Conceptual change in humans and machines* (pp. 157-185). Hillsdale, NJ: Erlbaum.

Humphrey, G. K., & Jolicoeur, P. (1993). An examination of the effects of axis foreshortening, monocular depth cues, and visual field on object identification. *The Quarterly Journal of Experimental Psychology, 46*(1), 137-159.

Im, C.-H., Gururajan, A., Zhang, N., Chen, W., & He, B. (2007). Spatial resolution of EEG cortical source imaging revealed by localization of retinotopic organization in human primary visual cortex.

Journal of neuroscience methods, 161(1), 142-154. doi:https://doi.org/10.1016/j.jneumeth.2006.10.008

Jeong, S. K., & Xu, Y. (2016). Behaviorally Relevant Abstract Object Identity Representation in the Human Parietal Cortex. *The Journal of Neuroscience, 36*(5), 1607-1619. doi:10.1523/jneurosci.1016-15.2016

Julian, J. B., Fedorenko, E., Webster, J., & Kanwisher, N. (2012). An algorithmic method for functionally defining regions of interest in the ventral visual pathway. *Neuroimage, 60*(4), 2357-2364. doi:10.1016/j.neuroimage.2012.02.055

Kar, K., Kubilius, J., Schmidt, K., Issa, E. B., & DiCarlo, J. J. (2019). Evidence that recurrent circuits are critical to the ventral stream's execution of core object recognition behavior. *Nature Neuroscience, 22*(6), 974-983. doi:10.1038/s41593-019-0392-5

Karnath, H.-O., Ferber, S., Rorden, C., & Driver, J. (2000). The fate of global information in dorsal simultanagnosia. *Neurocase, 6*(4), 295-306.

King, J.-R., & Dehaene, S. (2014). Characterizing the dynamics of mental representations: the temporal generalization method. *Trends in Cognitive Sciences, 18*(4), 203-210.

Koessler, L., Maillard, L., Benhadid, A., Vignal, J. P., Felblinger, J., Vespignani, H., & Braun, M. (2009). Automated cortical projection of EEG sensors: Anatomical correlation via the international 10–10 system. *Neuroimage, 46*(1), 64-72. doi:https://doi.org/10.1016/j.neuroimage.2009.02.006

Kravitz, D. J., Saleem, K. S., Baker, C. I., & Mishkin, M. (2011). A new neural framework for visuospatial processing. *Nature Reviews Neuroscience, 12*, 217. doi:10.1038/nrn3008

Kravitz, D. J., Saleem, K. S., Baker, C. I., Ungerleider, L. G., & Mishkin, M. (2013). The ventral visual pathway: an expanded neural framework for the processing of object quality. *Trends in Cognitive Sciences, 17*(1), 26-49.

Kriegeskorte, N., Mur, M., & Bandettini, P. (2008). Representational similarity analysis - connecting the branches of systems neuroscience. *Frontiers in Systems Neuroscience, 2*(4). doi:10.3389/neuro.06.004.2008

Krishnaswamy, P., Obregon-Henao, G., Ahveninen, J., Khan, S., Babadi, B., Iglesias, J. E., . . . Purdon, P. L. (2017). Sparsity enables estimation of both subcortical and cortical activity from MEG and EEG. *Proceedings of the National Academy of Sciences, 114*(48), E10465-E10474.

Liu, Y., Vogels, R., & Orban, G. A. (2004). Convergence of depth from texture and depth from disparity in macaque inferior temporal cortex. *Journal of Neuroscience, 24*(15), 3795-3800.

Luu, P., & Ferree, T. (2005). Determination of the HydroCel Geodesic Sensor Nets' average electrode positions and their 10–10 international equivalents. *Inc, Technical Note*, 1-11.

Oliver, Z. J., Cristino, F., Roberts, M. V., Pegna, A. J., & Leek, E. C. (2018). Stereo viewing modulates three-dimensional shape processing during object recognition: A high-density ERP study. *Journal of Experimental Psychology: Human Perception and Performance, 44*(4), 518.

Orban, G. A. (2011). The extraction of 3D shape in the visual system of human and nonhuman primates. *Annual review of neuroscience, 34*, 361-388.

Pitcher, D., Charles, L., Devlin, J. T., Walsh, V., & Duchaine, B. (2009). Triple Dissociation of Faces, Bodies, and Objects in Extrastriate Cortex. *Current Biology, 19*(4), 319-324. doi:https://doi.org/10.1016/j.cub.2009.01.007

Regev, T. I., Winawer, J., Gerber, E. M., Knight, R. T., & Deouell, L. Y. (2018). Human posterior parietal cortex responds to visual stimuli as early as peristriate occipital cortex. *European Journal of Neuroscience, 48*(12), 3567-3582.

Riddoch, M. J., & Humphreys, G. W. (1987). A case of integrative visual agnosia. *Brain, 110*(6), 1431-1462.

Riddoch, M. J., Humphreys, G. W., Akhtar, N., Allen, H., Bracewell, R. M., & Schofield, A. J. (2008). A tale of two agnosias: Distinctions between form and integrative agnosia. *Cognitive Neuropsychology, 25*(1), 56-92.

Romei, V., Driver, J., Schyns, P. G., & Thut, G. (2011). Rhythmic TMS over Parietal Cortex Links Distinct Brain Frequencies to Global versus Local Visual Processing. *Current Biology, 21*(4), 334-337. doi:https://doi.org/10.1016/j.cub.2011.01.035

Rosch, E., Mervis, C., Gray, W., Johnson, D., & Boyes-Braem, P. (2004). Basic objects in natural categories. *Cognitive Psychology: Key readings, 448*.

Takemura, H., Rokem, A., Winawer, J., Yeatman, J. D., Wandell, B. A., & Pestilli, F. (2016). A major human white matter pathway between dorsal and ventral visual cortex. *Cerebral Cortex, 26*(5), 2205-2214.

Tang, H., Schrimpf, M., Lotter, W., Moerman, C., Paredes, A., Ortega Caro, J., . . . Kreiman, G. (2018). Recurrent computations for visual pattern completion. *Proceedings of the National Academy of Sciences, 115*(35), 8835-8840. doi:10.1073/pnas.1719397115

Tarr, M. J., & Bülthoff, H. H. (1995). Is human object recognition better described by geon structural descriptions or by multiple views? Comment on Biederman and Gerhardstein (1993). *Journal of Experimental Psychology: Human Perception and Performance, 21*(6), 1494-1505.

Thomas, C., Kveraga, K., Huberle, E., Karnath, H.-O., & Bar, M. (2012). Enabling global processing in simultanagnosia by psychophysical biasing of visual pathways. *Brain, 135*(5), 1578-1585. doi:10.1093/brain/aws066

Van Dromme, I. C., Premereur, E., Verhoef, B.-E., Vanduffel, W., & Janssen, P. (2016). Posterior Parietal Cortex Drives Inferotemporal Activations During Three-Dimensional Object Vision. *PLOS Biology, 14*(4), e1002445. doi:10.1371/journal.pbio.1002445

Vaziri-Pashkam, M., Taylor, J., & Xu, Y. (2019). Spatial frequency tolerant visual object representations in the human ventral and dorsal visual processing pathways. *Journal of Cognitive Neuroscience, 31*(1), 49-63.

Wang, L., Mruczek, R. E. B., Arcaro, M. J., & Kastner, S. (2014). Probabilistic Maps of Visual Topography in Human Cortex. *Cerebral Cortex, 25*(10), 3911-3931. doi:10.1093/cercor/bhu277

Webster, M. J., Bachevalier, J., & Ungerleider, L. G. (1994). Connections of inferior temporal areas TEO and TE with parietal and frontal cortex in macaque monkeys. *Cerebral Cortex, 4*(5), 470-483.

Welchman, A. E. (2016). The human brain in depth: how we see in 3D. *Annual Review of Vision Science, 2*, 345-376.

Willenbockel, V., Sadr, J., Fiset, D., Horne, G. O., Gosselin, F., & Tanaka, J. W. (2010). Controlling low-level image properties: The SHINE toolbox. *Behavior Research Methods, 42*(3), 671-684. doi:10.3758/brm.42.3.671

Zachariou, V., Nikas, C. V., Safiullah, Z. N., Gotts, S. J., & Ungerleider, L. G. (2017). Spatial mechanisms within the dorsal visual pathway contribute to the configural processing of faces. *Cerebral Cortex, 27*(8), 4124-4138.

Zaretskaya, N., Anstis, S., & Bartels, A. (2013). Parietal cortex mediates conscious perception of illusory gestalt. *Journal of Neuroscience, 33*(2), 523-531.