Dynamic decoding of ongoing perception

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ABSTRACT

Decoding of perceptual and mental states using multivariate analysis methods has received much recent attention. It relies on selective responses to experimental conditions in single trials, aggregated across voxels. In this study, we show that decoding is also possible when the state of interest changes continuously over time. It is shown that both orientation and rotation direction of a continuously rotating grating can be decoded with high accuracy using linear dynamical systems and hidden Markov models. These findings extend the decoding results for static gratings and are of importance in the decoding of ongoing changes in mental state.

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Introduction

Various studies have shown that the (subjective) contents of perception can be decoded from functional magnetic resonance imaging (fMRI) data using multivariate analysis methods (Norman et al., 2006; Haynes and Rees, 2006). For example, groundbreaking work by Kamitani and Tong (Kamitani and Tong, 2005) has shown that the orientation of a static grating can be decoded with high accuracy. The possibility of decoding stimulus orientation from fMRI response has been hypothesized to rely either on biased sampling of cortical orientation columns (Kamitani and Tong, 2005; Swisher et al., 2010; Kriegeskorte et al., 2010) or on patterns of spatial organization at a coarser scale, e.g., due to influences of macroscopic blood vessels or globally unequal representations (Op de Beeck, 2010). Recent results suggest that both fine and coarse patterns of spatial organization might be responsible for successful decoding of stimulus orientation (Shmuel et al., 2010).

The possibility to probe internal states from distributed patterns of brain activity offers a new window into the brain and has led to novel insights about neural representations involved in various mental processes (Haxby et al., 2001; Kamitani and Tong, 2005; Haynes and Rees, 2005b; Thirion et al., 2006; Formisano et al., 2008; Miyawaki et al., 2008; Kay et al., 2008; Naselaris et al., 2009; Haynes, 2009; Hassabis et al., 2009; Chadwick et al., 2010; Reddy et al., 2010). However, to date, most decoding studies have focused on static decoding of single events in individual trials even though mental state is an ongoing process which evolves over time. The ability to decode continuously changing stimuli over time from distributed patterns of brain activity would truly enable tracking of how the internal state evolves as it is influenced by endogenous and exogenous controls.

Dynamic decoding has many applications, such as being able to track the temporal dynamics of bistable perception (Haynes and Rees, 2005b; Brouwer and van Leeuwen, 2007), decode the memory trace (Hassabis et al., 2009; Chadwick et al., 2010; Fuentemilla et al., 2010) or predict certain aspects of ongoing (subjective) perception (Miyawaki et al., 2008; Kay et al., 2008; Naselaris et al., 2009). This has been recognized by Haynes and Rees (Haynes and Rees, 2005b), who have shown that spontaneous changes in conscious experience during binocular rivalry can be decoded using linear discriminant analysis. In this paper, we demonstrate that time-series analysis methods are well suited for the dynamic decoding of ongoing mental processes.

Contrary to Haynes and Rees, we use a generative method that is able to track these ongoing changes through time by modeling the autocorrelations in the signal of interest, thereby achieving better decoding performance. Furthermore, we do not only focus on discrete changes in internal state, as is the case with spontaneous changes in bistable perception, but on continuous changes as well. In order to achieve these desiderata we presented three subjects with a moving grating that was continuously changing in terms of orientation direction and speed. We decoded both rotation angle and direction of the grating, thereby extending previous work on static decoding of perceived stimulus orientation (Kamitani and Tong, 2005) and rotational motion (Kamitani and Tong, 2006).
Material and methods

Subjects

Three healthy adults with normal or corrected-to-normal vision participated in this study. The study was approved by the local ethics committee and all subjects (authors MG, PK and FL) gave written informed consent.

Stimuli and experimental design

Visual stimuli were generated using MATLAB in conjunction with the Psychophysics Toolbox (Brainard, 1997) and displayed on a rear-projection screen using an LCD projector (EIKI, Rancho Santa Margarita, CA, USA). The experiment consisted of ten 180 s long runs which were each preceded by a 15 s long rest period. In each run, a rotating sine-wave annular grating (∼100% contrast, 1.5 cycles per degree, 5° eccentricity, inner annulus 3° in diameter) was presented, as shown in Fig. 1. The rotating grating was defined to have a different spatial phase between runs. Within a run, a variable angular velocity of ten to twenty degrees per second was used with an initial angular velocity of fifteen degrees per second. Angular velocity was modulated by a sine wave that consisted of 3, 5, or 7 cycles per run. In each run, rotation direction changed at constant intervals amounting to 3, 5, or 7 direction changes per run. The subject viewed the stimulus while maintaining central fixation and counting the number of changes in rotation direction throughout the experiment.

The discrete changes in direction and continuous changes in angular velocity make the decoding of rotation angle a non-trivial problem.

In a separate session, a standard retinotopic mapping experiment was conducted to delineate visual areas using a rotating wedge stimulus (Sereno et al., 1995). Subjects viewed a wedge, consisting of a flashing checkerboard pattern (3 Hz), first rotating clockwise for 9 cycles and then anticlockwise for another 9 cycles (at a rotation speed of 23.4 s/cycle).

In a third session, a functional localization experiment was used to localize area MT+. In order to localize voxels sensitive to linear or rotational motion, the subjects viewed the grating in different conditions: static non-drifting, static-drifting, and rotating non-drifting. Each run consisted of a rest block followed by the blocks defined by the different conditions. Each block was 15 s long and each run was repeated ten times.

MRI acquisition

Functional images were acquired with a Siemens 3T MRI system using a 32 channel coil for signal reception. For the main experiment, 1319 blood oxygenation level dependent (BOLD) sensitive functional images were acquired using a single shot gradient EPI sequence, with a repetition time (TR) of 1500 ms, echo time (TE) of 30 ms, isotropic voxel size of 2 × 2 × 2 mm, acquired in 26 axial slices in ascending order using a (GRAPPA) acceleration factor of 3. Dummy volumes were acquired at the beginning of each scan in order to account for T1 equilibration effects. A high-resolution anatomical image was acquired using an MP-RAGE sequence (TE/TR = 3.39/2250 ms; 176 sagittal slices, isotropic voxel size of 1 × 1 × 1 mm).

Functional MRI data preprocessing

Functional data were preprocessed within the framework of SPM8 (Statistical Parametric Mapping, http://www.fil.ion.ucl.ac.uk/spm/). Dummy scans were removed before preprocessing. Functional brain volumes were realigned to the mean image in order to correct for motion and the anatomical image was coregistered with the mean of the functional images. Data were high-pass filtered with a filter cutoff of 128 s, represented as percentage signal change and finally centered and scaled to have mean zero and unit variance.

In the present analysis we restricted ourselves to regions of interest in visual cortex. We performed retinotopic mapping to identify the boundaries of retinotopic areas in early visual cortex using well-established methods (Sereno et al., 1995; DeYoe et al., 1996; Engel et al., 1997). Freesurfer (http://surfer.nmr.mgh.harvard.edu) was used to generate inflated representations of the cortical surface from each subject’s T1-weighted structural image and to analyze the functional data of the retinotopic mapping session. Fourier-based methods were used to obtain polar angle maps of the cortical surface, on the basis of which the borders of visual areas (dorsal and ventral V1, V2 and V3 in both hemispheres) could be defined for each subject (Sereno et al., 1995). Area MT+ was localized by taking the most significant clusters obtained from a GLM contrast (static drifting + rotating − static conditions) while restricting the clusters to fall within area OCS of the SPM Anatomy toolbox. This area was delineated using a liberal probability threshold greater than zero in order to ensure the inclusion of motion-sensitive voxels for the decoding analysis. The area was warped into native space by applying the inverse normalization parameters to the mask.

Decoding analysis

In order to dynamically decode both grating orientation and rotation direction from the continuously rotating grating, we made use of time-series analysis methods. Assume that the state vector of interest $x = (x_1, \ldots, x_T)$ forms a Markov chain and is only indirectly observable via measurements $y = (y_1, \ldots, y_T)$. The joint density for this generative model is then given by

$$p(x, y) = p(x_1) \prod_{t=2}^{T} p(x_t | x_{t-1}) \prod_{t=1}^{T} p(y_t | x_t)$$

(1)

where the dependence on the model parameters $\theta$ is left implicit. Ultimately, we are interested in computing the most probable sequence of states $x^* = \arg \max_x p(x | y)$ for new observations $y$. This is achieved by estimating the model parameters $\theta$ from data acquired over multiple runs and inferring $x^*$ from measurements made in independent runs. Since the state is observed during training we can immediately estimate parameters from data instead of needing to estimate them using an expectation-maximization algorithm (Dempster et al., 1977).

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Decoding of grating orientation and rotation direction requires inference about a continuous mental state (orientation) or a discrete mental state (direction). In case of continuous mental orientation, we assume that both the state and measurement variables are Gaussian with the mean being linearly dependent on the conditioning variables. That is, we have

\[
\begin{align*}
    p(x_i) &= N(x_i; \mu, \Sigma) \\
    p(x_i | x_{i-1}) &= N(x_i; Ax_{i-1}, Q) \\
    p(y_i | x_i) &= N(y_i; Cx_i, R)
\end{align*}
\]

with parameters \( \theta = (\mu, A, Q, C, R) \). This model is known as a linear dynamical system (LDS) (Roweis and Ghahramani, 1999) where decoding of \( x \) is realized using the Kalman smoother. If, in contrast, the underlying mental state is discrete, such as in case of rotation direction or spontaneous changes during bistable perception, we obtain the hidden Markov model (HMM) (Roweis and Ghahramani, 1999) where the state variables are multinomial random variables and \( x \) is computed by the Viterbi decoder. For binomial state variables with \( x_i \in \{0, 1\} \), the distributions are defined by

\[
\begin{align*}
    p(x_i = 1) &= m \\
    p(x_i = 1 | x_{i-1}) &= \theta_0^{1-x_{i-1}} \theta_1^{x_{i-1}} \\
    p(y_i | x_i) &= N(y_i; \mu_0, R_0)^{(1-x_i)} N(y_i; \mu_1, R_1)^{x_i}
\end{align*}
\]

with parameters \( \theta = (m, \mu_0, \mu_1, R_0, R_1) \) with \( k \in \{0, 1\} \). All algorithms have been implemented in MATLAB 7 (Mathworks, Natick, MA, USA). For the HMM a small diagonal term of \( 10^{-3} \) was added to the covariance matrices \( R_k \) in order to avoid numerical stability issues.

In order to take into account the hemodynamic lag, for both the LDS and the HMM, measurements \( y_t \) associated with a state \( x_t \) at a certain point in time were given by the BOLD response within the volume acquired at a six second delay relative to stimulus onset \( t \).

In order to estimate the angle \( \alpha_t \), we used a linear dynamical system where the state vector is given by \( x_t = (\sin(\alpha_t), \cos(\alpha_t))^T \). This transformation is required since angle itself is a periodic variable which should be modeled using techniques from circular statistics (Fisher, 1996; Mardia and Jupp, 1999). The sine–cosine transformation allowed us to use standard time-series analysis methods.

Furthermore, since a grating is mirror symmetric, a full rotation is achieved after a 180° change in angle such that the average absolute deviation between the real angle and a random angle will be 45°. Decoding performance was estimated by computing the mean absolute deviation (MAD) between the real and predicted angle of the rotating grating. In order to estimate rotation direction, we used a hidden Markov model where the state \( x_t \in \{0, 1\} \) denotes clockwise or counter-clockwise rotation. Decoding performance was estimated by computing the classification error, that is, the proportion of volumes that have been assigned to the incorrect rotation direction.

In order to improve the efficiency of inference and to prevent overfitting we restricted the number of voxels that act as observations. We achieved this by ranking individual voxels in terms of the correlation between their BOLD timecourse and the timecourse(s) of interest (sine and cosine of the angle or rotation direction). In order to prevent circularity issues (Kriegeskorte et al., 2009), we used an outer and inner cross-validation approach. In the outer cross-validation, individual runs (test data) were decoded by means of probabilistic inference using a model that was estimated from data in the nine remaining runs (training data). In the inner cross-validation approach, eight out of nine runs in the training data were used to rank voxels according to their correlation with the signal timecourse(s) of interest. This ranking was used to identify the optimal number of voxels according to decoding performance on the remaining run in the test data. The identified voxels were used to train the model on all training data. This model was subsequently used in the outer cross-validation to produce decoding results for the test data. Final decoding performance was estimated by computing the average decoding performance over each of the ten runs. See Fig. 2 for a description of the decoding analysis.

In order to examine the differences in decoding performance between regions of interest, we have also analyzed decoding performance per region. In this case, in order to be able to compare decoding performances, a fixed number of voxels was used as the basis for decoding.

Results

Decoding of grating orientation

Fig. 2 depicts the orientation decoding results for all three subjects using the outer and inner cross-validation approach described above. Panel 3A shows the real and predicted cumulative angles (i.e., predicted orientations while taking into account full rotations) for the three subjects across all runs as compared with a random prediction that is obtained by ignoring the observed BOLD responses. The mean absolute deviations between the angle of the real and predicted grating orientation were 14.56° ± 0.80° SEM, 14.52° ± 0.56° SEM and 15.61° ± 0.71° SEM for subjects MG, PK and FL respectively, which is well below the chance level of 45°. All three subjects showed a weak positive correlation between the absolute deviation and the angular velocity (\( r = 0.28, r = 0.29 \) and \( r = 0.22 \)) which implies that the
accuracy of the estimates decreases as the rotation speed of the grating increases.

In order to examine how MAD changes as a function of the number of used voxels, we used the inner cross-validation results. That is, the corresponding estimates obtained per fold were averaged to produce the curves of interest for three subjects, as shown in Panel 3.B. The dashed vertical lines depict the optimal number of voxels for individual runs in the inner cross-validation. A minimal MAD was reached at about 200 included voxels.

Finally, Panel 3.C shows the voxels which were used for decoding the direction. The contours delineate dorsal and ventral visual areas V1, V2 and V3 as well as area MT+. The heat maps denote how often each voxel was used for decoding, averaged over cross-validation folds. Selected voxels extend from V1 up to and beyond V3 with dorsal areas being more prevalent than ventral areas, which could be associated with the performance asymmetry between the upper and lower visual field (Levine and McAnany, 2005) or due to differences in susceptibility artifacts between dorsal and ventral areas (Winawer et al., 2010).

Decoding of rotation direction

Fig. 4 depicts the direction decoding results for all three subjects using the inner and outer cross-validation approach described above. Panel 4A shows the real and predicted rotation directions for the three subjects in the first five runs. Classification error was 0.37, 0.34 and 0.41 for subjects MG, PK and FL respectively. Subjects showed no or a very weak positive correlation between the classification error and the angular velocity ($r = 0.05, r = 0.12$ and $r = -0.01$). In order to examine how classification error changes as a function of the number of used voxels, we used the inner cross-validation results.

Panel 4B depicts the curves of interest for three subjects. The dashed vertical lines depict the optimal number of voxels for individual runs in the inner cross-validation. A minimal error was reached at about ten included voxels. Panel 4C indeed shows that a small number of voxels are selected, mostly outside of early visual areas or area MT+. In general, rotation direction seems much harder to decode than grating orientation. The variability of the number of voxels which are selected in the inner cross-validation (cf. Panels 3.B and 4.B) also indicates decoding of direction is less robust than decoding of orientation.

Region of interest analysis

In order to identify how visual areas independently contribute to the decoding of grating orientation and rotation direction, we have used the functional localizers that have been acquired in independent sessions. In order to allow comparison of the contributions for each visual area, we used the fifty voxels whose BOLD response correlated most strongly with the signal(s) of interest. Fig. 5 shows the decoding results on the flattened cortical surface for each subject.

For grating orientation, decoding performance, averaged over dorsal and ventral as well as left and right hemisphere regions for all subjects, decreased when moving downstream from V1 to V3 (MADs of $30^\circ \pm 3^\circ$ SEM, $31^\circ \pm 3^\circ$ SEM and $34^\circ \pm 4^\circ$ SEM for areas V1, V2 and V3, respectively). This matches the decoding results of Kamitani and.

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Tong (2005) and is consistent with the poorer orientation selectivity in higher visual areas, as shown in animal studies (Vanduffel et al., 2002). Area MT+ did not allow decoding of grating orientation (MAD of 43° ± 1° SEM), which is also consistent with previous findings (Kamitani and Tong, 2005). Dorsal areas (MADs of 30° ± 2° SEM, 29° ± 2° SEM and 32° ± 2° SEM for areas V1, V2 and V3, respectively).

**Fig. 4.** Predicted rotation directions for the three subjects. Panel A shows the decoding result for first five runs. Panel B shows the classification error as a function of the number of used voxels where error bars denote standard error of the mean. Dashed vertical lines denote the number of voxels that are selected per cross-validation fold. Panel C shows the correlations between the signal of interest and those voxels which have been selected in the inner cross-validation to produce the final decoding results.

**Fig. 5.** Decoding results separately computed for visual areas V1, V2, V3 and MT+ for the three subjects. Panel A shows angle decoding results where color codes for decoding performance (45° — MAD). Panel B shows direction decoding results where color codes for classification accuracy (1 — classification error). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

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Fig. 6. Polar plots for the angle deviation as a function of orientation where orientations are binned into 30° windows with 20° overlap. Results are shown for all three subjects in ventral and dorsal regions of primary visual area V1 for both the left and right hemisphere.
performed somewhat better than ventral areas (MADs of 30°±4° SEM, 32°±4° SEM and 35°±4° SEM for areas V1, V2 and V3, respectively).

For rotation direction, decoding performance per region of interest was quite low. Still, we could observe decreases in performance in the downstream direction when dorsal and ventral as well as left and right hemisphere regions were pooled (classification errors of 0.37, 0.42 and 0.43 for areas V1, V2 and V3, respectively). Area MT+ now also became involved with an average classification error of 0.41.

We also examined whether individual regions showed a particular bias for certain grating orientations. Fig. 6 shows that there is some variability in the decoding of certain orientations in visual area V1, both within and between subjects. However, we have found no clear correspondences with previously reported orientation anisotropies in early visual cortex (Furmanski and Engel, 2000; Mannion et al., 2010).

**Static versus dynamic decoding**

In order to substantiate our claim that the decoding of ongoing mental state is facilitated by the use of dynamic instead of static decoding methods, we performed a comparative analysis. The static decoder was obtained simply by removing the autocorrelations for the state variable at neighboring timepoints. That is, we forced the matrix A to be zero and the transition probabilities $a_0$ and $a_1$ to be 0.5 during parameter estimation for the LDS and the HMM, respectively.

Fig. 7 demonstrates the decoding of mental state using randomly selected voxels in area V1. Panel 7.A shows an example of decoding of the sine and cosine of the rotation angle using a static decoder (blue line) and a dynamic decoder (red line). These results demonstrate that the dynamic decoder effectively performs an adaptive smoothing of the time-series due to the intrinsic autocorrelations. Panel 7.B shows that the dynamic decoder indeed improves on the static decoder in terms of MAD performance. The effects are even more salient for the decoding of rotation direction. Panel 7.C shows an example of decoding the rotation direction using a static decoder and a dynamic decoder. The static decoder completely fails due to the independence assumption between neighboring timepoints. Classification error is also substantially lower for the dynamic decoder (Panel 7.D). Subject PK, who performed best in previous analyses, now displays the worst decoding performance. This can be explained by the fact that those voxels which allowed decoding before may have been excluded by the random selection of voxels in area V1.

**Discussion**

In this paper, we have shown that dynamic decoding of ongoing mental state can be achieved using time-series analysis methods. First, it was shown that grating orientation can be decoded continuously by means of a linear dynamical system where the grating orientation is inferred using a Kalman smoother. Second, it was shown that rotation direction can be decoded using a hidden Markov model where the rotation direction is inferred using Viterbi decoding. Our comparison between static and dynamic decoding methods shows that the decoding of ongoing internal state from BOLD response is improved by employing dynamic decoding methods. This paves the way for decoding of ongoing perception in more ecological settings, such as viewing of movies (Hasson et al., 2004), as well as decoding of ongoing mental state which arises from internal processes instead of from external stimulation (Haynes and Rees, 2005a; Haynes, 2009). In the latter case, the state itself cannot be observed and requires the use of an expectation-maximization algorithm when estimating model parameters.

Even though both grating orientation and rotation direction could be decoded from BOLD response, results indicate that the former is...
much easier to decode than the latter. Figs. 3B and 4B show that the decrease in error is both more pronounced and more consistent for gratings orientation compared with rotation direction. The improved consistency follows from the fact that results are more comparable between and within subjects. Within subjects, the results for each cross-validation fold are more similar, as evidenced both by the smaller error bars as well as by the fact that the optimal number of voxels used for decoding is more similar between folds. Improved consistency also follows from the voxels selected for decoding as shown in Figs. 3C and 4C. Clusters of voxels in early visual cortex correlated strongly with gratings orientation whereas the voxels selected to decode rotation direction were more dispersed throughout the measured brain volume. The fact that orientation was easier to decode than rotational motion is in line with previous findings (Kamitani and Tong, 2005, 2006) and could be due to differences in spatial anisotropies between orientation and direction-selective neurons. Swisher et al. (2010) provide a nice account of the orientation biases that are present in the BOLD signal at multiple spatial scales.

The region of interest for analysis for decoding, depicted in Fig. 5B, shows that early visual cortex and area MT+ did allow for the decoding of rotation direction. Here, area MT+ outperformed early visual areas for subjects MG and PK while the converse was true for subject FL. Note however that it remains problematic to directly compare classification accuracy between different areas of the brain. For example, sampling from voxels in area V1, which is estimated to be about 3 times larger than MT, may in and of itself lead to a higher signal-to-noise ratio at the area level (Seresen and Boynton, 2007). Note further that there is a disparity between these results and the earlier decoding analysis in terms of selected voxels and their associated performance. This could indicate that the employed correlation-based feature ranking criterion may be suboptimal for selecting voxels that respond well to rotation direction.

For subject FL, additional information with respect to orientation was present in regions anterior to the early retinotopically defined visual cortical areas. While these areas are likely to be tuned for more complex stimulus properties than orientation, they may still show a response bias that can be picked up by the decoding algorithm. Retinotopic maps are found throughout the visual dorsal stream (Silver and Kastner, 2009) and these maps are known to exhibit unequal sampling of different orientations in particular parts of visual space (Sasaki et al., 2006).

In this paper, we have used linear dynamical systems and hidden Markov models in order to demonstrate that dynamic decoding of ongoing mental state from BOLD data is feasible. It should be noted however that the rate of stimulus change as used in this paper was quite slow. A weak positive correlation between decoding error and angular velocity was observed but it remains an open question how decoding performance is affected by more rapid stimulus changes in the presence of autocorrelations.

More sophisticated methods for time-series analysis could further improve decoding performance. One way to improve results is to use more complex generative models that provide a more natural representation of the phenomena we are trying to model. This can either be achieved by relaxing the Gaussianity assumptions, by introducing additional hidden variables, or by making other independence assumptions (Barber and Cemgil, 2010). Another way to improve results is to use a more principled approach to voxel selection, for example by means of dimensionality reduction techniques (Schölkopf et al., 1998) or by embedding the selection process directly within the employed inference algorithms, e.g., using automatic relevance determination (Beal, 2003). Finally, results may be improved by including a forward model of the hemodynamic response (Makni et al., 2008).

Dynamic decoding has several potential benefits compared to static decoding since it gives better insight into the temporal dynamics of ongoing mental state. This possibility to track mental state over time becomes especially important with the advent of real-time fMRI (DeCharms, 2008) where BOLD data is analyzed in an online manner which has applications in brain–computer interfacing and brain-state dependent stimulation. The aim of this paper is to encourage the use of time-series analysis methods for the decoding of ongoing mental state. Our results on the decoding of gratings orientation and rotation direction from BOLD response show that such methods are warranted whenever decoding is applied within a paradigm that is characterized by intrinsic temporal dynamics.

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