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Human visual and parietal cortex encode visual choices independent of motor plans

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ABSTRACT

Perceptual decision-making entails the transformation of graded sensory signals into categorical judgments. Often, there is a direct mapping between these judgments and specific motor responses. However, when stimulus–response mappings are fixed, neural activity underlying decision-making cannot be separated from neural activity reflecting motor planning. Several human neuroimaging studies have reported changes in brain activity associated with perceptual decisions. Nevertheless, to date it has remained unknown where and how specific choices are encoded in the human brain when motor planning is decoupled from the decision process. We addressed this question by having subjects judge the direction of motion of dynamic random dot patterns at various levels of motion strength while measuring their brain activity with fMRI. We used multivariate decoding analyses to search the whole brain for patterns of brain activity encoding subjects' choices. To decouple the decision process from motor planning, subjects were informed about the required motor response only after stimulus presentation. Patterns of fMRI signals in early visual and inferior parietal cortex predicted subjects' perceptual choices irrespective of motor planning. This was true across several levels of motion strength and even in the absence of any coherent stimulus motion. We also found that the cortical distribution of choice-selective brain signals depended on stimulus strength: While visual cortex carried most choice-selective information for strong motion, information in parietal cortex decreased with increasing motion coherence. These results demonstrate that human visual and inferior parietal cortex carry information about the visual decision in a more abstract format than can be explained by simple motor intentions. Both brain regions may be differentially involved in perceptual decision-making in the face of strong and weak sensory evidence.

Introduction

Our brain continuously transforms noisy and incomplete sensory signals into categorical judgments about the state of the outside world. Much progress has been made in understanding the neural mechanisms underlying such decision-making processes. Monkey neurophysiology (Gold and Shadlen, 2000; Roitman and Shadlen, 2002; Romo et al., 2002; Salinas et al., 2000; Shadlen and Newsome, 2001) and human neuroimaging studies (Donner et al., 2009; Heekeren et al., 2004, 2006; Ho et al., 2009; Tosoni et al., 2008) provide converging evidence that, in the face of uncertainty, the brain produces perceptual choices by accumulating weak signals from sensory cortical areas.

It has, however, remained largely unknown how perceptual choices are encoded when they are decoupled from action planning. Most previous studies directly mapped perceptual choices (e.g. upward vs. downward motion) onto motor responses (e.g. right vs. left button press) and in that way treated perceptual decision-making as a problem of action selection (Freedman and Assad, 2011; Gold and Shadlen, 2007). Consequently, the decision process was reflected in neuronal activity in sensorimotor and motor brain regions, both in macaque monkeys (Horwitz and Newsome, 1999; Kim and Shadlen, 1999; Salinas and Romo, 1998; Shadlen and Newsome, 2001) and in humans (Donner et al., 2009; Tosoni et al., 2008). In monkeys, a subset of parietal neurons also encoded perceptual choices when the decision was decoupled from the motor response (Bennur and Gold, 2011), but this study focused on a single brain area in the macaque. It has remained an open question how such abstract perceptual

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choices are represented in the human brain and in particular which brain regions participate in the decision process.

Although a number of recent neuroimaging studies have characterized neural substrates of visual perceptual choice in the human brain (Domenech and Dreher, 2010; Heekeren et al., 2004, 2006; Ho et al., 2009; Kayser et al., 2010a, 2010b; Kovács et al., 2010; Li et al., 2009; Liu and Pleskac, 2011; Ploran et al., 2007; Tosoni et al., 2008), the vast majority of these studies focused on which brain areas are "active" during the decision process. Such activity may reflect a number of processes associated with decision-making (e.g., attention, arousal, conflict monitoring) which are not specific to the decision itself. For that reason, it has remained largely unknown which regions of the human brain are specifically involved in encoding perceptual decision signals and thus may participate in forming the subjects' specific choices (e.g. motion up vs. motion down). Although a causal contribution of a particular brain region can only be investigated with lesion and neurostimulation techniques (Hanks et al., 2006), a distinction of choice-specific from non-specific brain signals would strongly contribute to our understanding of the neural processes underlying perceptual decision-making.

Here, we used fMRI to investigate choice-encoding by applying multivoxel pattern analysis to human brain signals. Subjects formed decisions about the net motion direction in dynamic random dot patterns of various strengths spanning psychophysical threshold. To pinpoint brain regions that encode choices independent of the corresponding motor plans, subjects were informed about the association of choice and response only after stimulus presentation by means of a stimulus–response mapping screen. The use of a response-mapping screen that varies pseudo-randomly from trial to trial effectively decorrelates specific perceptual choices ("up" vs. "down") from the specific motor responses (left vs. right button press). This obviates the need to jitter events in time for separating activity patterns encoding choices and motor responses. Effectively, for one particular choice roughly the same number of trials carry information about each button press, annihilating the classifiers' ability to separate the perceived direction of motion based on the button presses. For example, while one choice may be directly followed by a right button press on some trials, it will be followed by a left button press on approximately the same number of trials. For that reason, the classifier will not pick up any motor response-specific brain signals, but only choice-specific brain signals.

In addition to measuring the levels of overall fMRI responses, we targeted brain regions carrying specific information about subjects' upcoming choices by means of a "searchlight" decoding analysis scanning the entire brain (Kriegeskorte et al., 2006; Haynes et al., 2007). We applied effects-of-interest group analyses across different levels of sensory evidence to identify decision-related brain signals at the group level. These statistical contrasts have the advantage of being unbiased towards the amount of choice-selective information across different levels of sensory evidence. In other words, our approach makes no specific assumptions about where to expect meaningful patterns of brain activity and how the amount of information changes across different levels of sensory evidence.

Materials and methods

Subjects

25 neurologically healthy volunteers participated in the study. Three participants were subsequently excluded from the analysis due to strong decision biases in the scanning session (see below). The remaining 22 participants (11 female, mean age: 25.23, SD: 3.69 years) were right-handed and had normal or corrected-to-normal vision. Subjects were paid 7 € per hour for training and 10 € per hour for the scanning session. All participants provided written informed consent. The study was approved by the ethics committee of the Max-Planck Institute for Human Cognitive and Brain Sciences (Leipzig).

Stimuli and procedure

Stimuli were generated using Matlab (MathWorks) and the Cogent Toolbox (http://www.vislab.ucl.ac.uk/Cogent). For the training sessions, stimuli were presented on a TFT monitor at a frame rate of 60 Hz in a dimly lit room. In the MR scanning session, stimuli were projected with an LCD projector (60 Hz frame rate) onto a translucent screen in the bore of the scanner and viewed through a surface mirror mounted on the head coil.

All stimuli were drawn in white on black background unless noted otherwise. Random dot motion (RDM) kinematograms were created in a square region, but only dots in an annular region were presented on the screen (central aperture diameter: 3 dva, annulus diameter: 15 dva). Each dot (diameter: 0.10 dva) was assigned a fixed direction of motion from one out of twelve equally spaced possible directions to prevent judgments to be based on only a small number of dots that moved straight in a target direction. This means that even for zero coherence, 8.33% coherent motion was present, but the net coherence in a given direction was indeed zero. Dots that left the square region were redrawn on the opposite side of the square. Coherence was varied by the percentage of dots moving coherently upwards (90°) or downwards (270°). Average dot density was 4 dots/dva^2 and dot speed was 6°/s. To reduce the possibility of tracking individual dots, each dot was assigned a halflife of 100 ms.

The task of the subjects was to judge whether the net global motion was upward or downward and to indicate this judgment by pressing a button after stimulus offset and following the stimulus–response mapping provided on the current trial. The association between perceptual choice (upward vs. downward motion) and motor response (left- vs. right-hand button press) was varied from trial by trial by the use of a "response-mapping screen" presented after the RDM stimulus. This allowed to decouple movement-selective from choice-selective neuronal activity during decision-formation (Bennur and Gold, 2011; Haynes et al., 2007; Rahnev et al., 2011) and decorrelated choice-related and motor response-related BOLD signals that would otherwise be difficult to separate due to the sluggish BOLD response. The response-mapping screen consisted of two arrows presented left and right of fixation (arrow: 0.38 dva width × 1 dva height, distance from fixation: 1 dva), one arrow pointing up and the other pointing down. The arrow that matched the subjects' judgment of the motion direction indicated the hand with which they had to respond.

We used an interrogation protocol in which the decision time is controlled by the experimenter rather than by the subject (Bogacz et al., 2006). The sequence of events within one trial is illustrated in Fig. 1a. Each trial started with a central fixation cross. After a brief cue (yellow fixation cross; onset: 1000 ms, offset: 500 ms prior to RDM onset), RDM stimuli were shown for a fixed duration of 1500 ms, during which the subject formed a decision. Stimulus presentation was followed by the response-mapping screen for 1500 ms, and a variable intertrial interval of 1000, 3000, or 5000 ms. Thus, the total trial duration was on average 6 s. During the presentation of the response-mapping screen subjects could indicate their decision by pressing a button with the left or right index finger. In training sessions, subjects received visual feedback by a change of the fixation cross to green or red, indicating correct and incorrect responses, respectively. In the scanning session, subjects did not receive feedback on a trial-by-trial basis, but were informed about their performance after each experimental run to increase their motivation.

All participants were trained for 2.5 h in two sessions prior to scanning to stabilize performance and reduce intrinsic decision biases. Inexperienced subjects were trained to maintain fixation using the Troxler fading illusion (Troxler, 1804). For training sessions, the method of

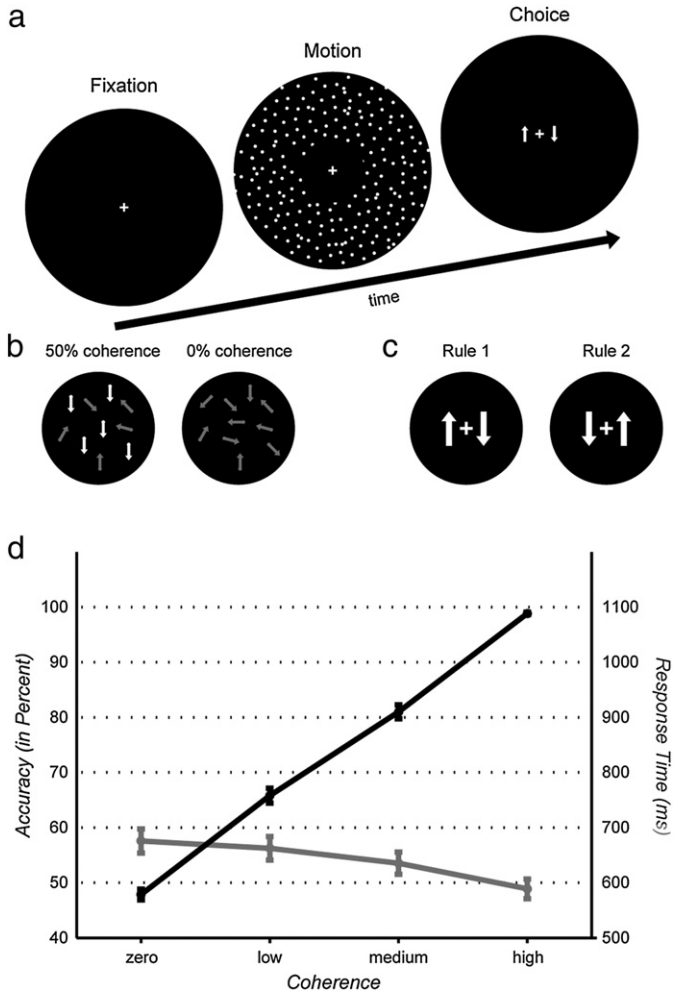

Fig. 1. Experimental design and behavioral results. (a) Random dot motion stimuli of varying coherence were shown for 1500 ms, followed by a "response-mapping screen" at which subjects had to indicate whether the majority of dots was moving up or down. (b) The coherence of the dots varied between 0% and 50%, with two individually calibrated levels around 65% and 85% threshold. (c) The response-mapping screen was introduced to decorrelate motion directions and motor plans. (d) Behavioral results indicate that behavioral accuracies well matched the expected levels of performance. Also response times varied with motion coherence. Error bars denote standard error of the mean.

constant stimuli was used (3.125%, 6.25%, 12.5%, 25%, 50% motion coherence). Trials from the second session were fit with a Weibull function to determine each subject's perceptual 65% and 85% threshold. In the scanner prior to the main experiment, subjects performed 64 trials of a behavioral calibration block using the QUEST procedure (Watson and Pelli, 1983) to estimate their 75% threshold and manually correct for small changes in threshold between sessions. In the final scanning experiment, each subject was shown four levels of motion coherence: 50% coherence, 0% coherence, and the two individually adjusted levels that yielded around 65% and 85% correct performance (mean coherence levels: 7.86%, SD: 1.28, and 13.41%, SD: 2.11). These four levels were chosen to achieve performance variations from 50% accuracy (chance level) to 100% accuracy in each individual subject. The label 'upward' or 'downward' motion was assigned randomly to the 0% coherence condition. Subjects were not explicitly informed about the fact that a condition with no coherent motion was included, but they were instructed to always give a response. Subjects with a strong decision bias were excluded when their point of subjective equality for upward and downward motion was shifted left- or rightward to an extent that exceeded the low coherence condition.

Each experimental run consisted of 8 trials per direction of motion and coherence, resulting in 64 trials per run lasting 6 min 24 s. Participants completed between eight and ten experimental runs, i.e. they completed a total number of 512 to 640 trials. Trials were presented in pseudo-randomized order. The order was chosen to make the trial sequence unpredictable, and intertrial intervals were chosen to optimize efficiency of the statistical design (Dale, 1999). Eye movements were monitored in all subjects using a 50 Hz MRI-compatible video-based system (Sensorimotor Instruments, Teltow, Germany). After the experiment was finished, subjects underwent a localizer run to isolate brain regions that respond preferentially to coherent compared to random motion which should include the motion-selective region MT+/V5 (Braddick et al., 2001; Rees et al., 2000).

MRI data acquisition

All imaging was conducted on a 3 Tesla Siemens TIM Trio scanner (Siemens, Erlangen) equipped with a 12 channel head coil. During the behavioral calibration of the subject in the scanner, a T1-weighted image (MPRAGE) was collected as a high-resolution anatomical reference (TE: 2.52 ms, TR: 1900 ms, flip angle: 9°, FOV: 256 mm, matrix size: 256×256, slice thickness: 1 mm, 192 slices). T2*-weighted gradient-echo echo-planar images were collected as functional images for the experimental runs and the motion localizer (TE: 30 ms, TR: 2000 ms, flip angle: 90°, FOV: 192 mm, matrix size: 64×64, slice thickness: 3 mm, interslice gap: 0.3 mm, 33 slices, ascending sequence).

Univariate analysis of fMRI data

We applied two lines of data analysis, one with a standard mass-univariate general linear model (GLM) and one with multivariate classification. For univariate analyses, functional images were preprocessed by spatial realignment, slice-timing correction, spatial warping to an average anatomical subject template using DARTEL (Ashburner, 2007), affine transformation to MNI space and spatial smoothing (Gaussian kernel with 6 mm FWHM). These steps were performed in the SPM8 framework (http://www.fil.ion.ucl.ac.uk/spm/). After preprocessing, the BOLD signal of each voxel in each subject was estimated with two regressors in a general linear model: one baseline regressor for RDM stimulus presentation and one linear parametric regressor for different levels of motion coherence. Stimulus onsets and durations were modeled with a boxcar function convolved with a canonical hemodynamic response function (HRF). The second regressor yielded a parameter estimate that expressed a positive or negative relationship of the BOLD signal of each voxel with different levels of motion coherence. All models included an intrinsic temporal high-pass filter of 1/128 Hz to correct for slow scanner drifts. Six additional movement parameters were included to explain variance introduced through head motion. Parameter estimates of each individual's linear parametric regressor were submitted to a group t-test, yielding brain regions where the BOLD signal correlated positively or – for negative t-values – negatively with coherence.

The data from the motion localizer was preprocessed similarly, but without warping and spatial smoothing. One regressor for coherent motion and one for random motion plus six additional head movement regressors were entered into a GLM. For each subject, we defined area MT+/V5 based on a combination of anatomical criteria (Dumoulin et al., 2000), the contrast "coherent motion>random motion" at $p<0.05$ uncorrected, and manual voxel selection. For later comparison to our group results, we took these anatomical masks, spatially normalized them and combined them to an image of the sum of all these masks, ranging in values from 1 to the number of subjects. This yielded a relatively large mask of 1268 voxels.

Multivariate classification analysis I: decoding the stimulation

For multivariate classification, functional images were also preprocessed by spatial realignment and slice-timing correction, but excluding warping, transformation to MNI space and spatial smoothing (these steps were performed only after multivariate classification to preserve the fine-scale spatial information that contribute to multivoxel pattern analysis). After preprocessing different GLMs were created as above, depending on the conditions of interest. For each GLM, we modeled only the regressors of interest, i.e. trials without response and motion regressors, because in our experience a full model can lead to reduced classification performance, probably because variance that is important for pattern information is stolen by other regressors, even if they are largely uncorrelated across trials. To classify the *physical* motion direction of the stimulus depending on the coherence level, eight regressors were created where motion directions (up and down) were modeled separately for each of the four levels of motion coherence. In this way, for each experimental run and each condition of interest a parameter estimate was achieved that could later be used for classification analyses.

To identify brain regions that not only vary with motion coherence, but carry information about the direction of motion, a searchlight classification analysis (Kriegeskorte et al., 2006) was performed on each participant using a leave-one-run-out cross validation approach (Haynes et al., 2007) to detect informative local spatial fMRI patterns across the whole brain. This procedure has previously been explained in greater detail (Kahnt et al., 2010; Tusche et al., 2010). For classification, we used a linear support vector machine in the implementation of LIBSVM 2.86 (Chang and Lin, 2011) with a cost parameter of $c = 1$. All voxels surrounding a given voxel within a sphere of 10 mm radius were included in a searchlight. Parameter estimates of one condition from voxels within a searchlight served as a pattern vector for this condition. Pattern vectors for two conditions of interest from all but one run were used to train a classifier to distinguish between these two conditions, e.g. upwards vs. downwards motion for high-coherence stimuli. The classifier was then used to predict the categories of the patterns from the left-out run. This procedure was repeated iteratively for each run, yielding a mean cross-validation prediction accuracy for the searchlight across the whole experiment. The central voxel of the searchlight was then assigned this cross-validation accuracy. The whole process was repeated for each voxel in the brain, generating a map of local classification accuracies across the whole brain.

Searchlight classification of physical stimulation yielded four accuracy maps per subject, each representing the informational content for the stimulation for each level of motion coherence. After all of these maps were spatially warped, transformed to MNI space and spatially smoothed (see above), they were submitted to a group repeated-measures ANOVA to identify brain regions where the prediction accuracy was significantly different from chance (50% accuracy) in at least one of the four conditions. Post-hoc statistical tests were carried out on peak voxels of each cluster.

Multivariate classification analysis II: decoding the decision

In addition to decoding the motion direction of the stimulus, we were interested in subjects' *choices* about motion stimuli. For this purpose we used a very similar approach as above, but this time first created eight GLM-regressors, each of which reflected one of both directions of motion indicated by the subject, i.e. the subject's decision, separately for all four levels of motion coherence (e.g. perceived motion up vs. perceived motion down at zero coherence). Again a searchlight classification analysis was carried out separately for each of the four levels of motion coherence where we searched for patterns of brain activity that carried information about the outcome of the choice (up vs. down). For each subject this resulted in four accuracy maps that were spatially warped, transformed to MNI space and spatially smoothed, and submitted to a group repeated-measures ANOVA (see above).

Results

Behavioral and eye-tracking results

Mean reaction times and accuracies across different levels of motion coherence are displayed in Fig. 1d. As can be seen, the accuracy values across all subjects were in good agreement with the expected performance levels. A repeated-measures ANOVA across all four coherence levels confirmed that accuracy was modulated by the coherence of the RDM stimulus ($F_{(3,63)} = 581.89$, $p < 0.001$). Furthermore, reaction times decreased with motion coherence ($F_{(3,63)} = 61.76$, $p < 0.001$), although the stimulus was presented for a fixed duration, there were no speed instructions to the subject (interrogation protocol), and subjects were not immediately given a stimulus–response assignment.

One might be concerned that even with the use of a response-mapping screen choices and motor responses were not fully separated, for example because subjects chose more often "up" with the right than with the left hand. In this scenario, multivariate classification analyses could possibly pick up motor response-specific brain signals that are only seemingly choice-specific. To estimate whether subjects' left and right button presses could be predicted from their choices for up and downward motion, we ran a two-tailed binomial test testing for a correspondence between choices and button presses for each subject separately. Only one out of 22 subjects approached significance in responding more often right when the choice was up than when it was down (54.92% of all valid trials, $p = 0.067$, all other subjects $p > 0.221$). Thus, subjects rarely, if ever, chose their button press depending on their choice of motion direction.

Eye movements were defined by a deviation from fixation that exceeded 2 dva and that lasted longer than 200 ms, in addition to manual selection because of occasional noise bursts in the eye-tracking signal. Due to technical failure only eye movement data from 14 subjects was available for eye-tracking analysis. We found only a small fraction of trials with saccades (number of saccades per subject: 1.17, SD: 1.03). We additionally tested for significant deviations in mean eye position between our conditions of interest. Possibly, small eye movements or deviations from fixation could explain our pattern of results. We estimated the mean eye position along the x- and y-axis for each trial separately and averaged these trial estimates according to the motion coherence and the choice of the subject. We then ran two separate two-way repeated measures ANOVAs with the factors "coherence" and "choice", and with the dependent variable being the deviation along the x- and y-axis, respectively. A main effect of choice or an interaction of choice and coherence could provide information that may be picked up by a classifier to predict choices or changes in choices with level of coherence, respectively. For the x-axis, we found no significant main effect or interaction (all $F < 1$). For the y-axis, we found a main effect of coherence ($F_{(3,39)} = 3.84$, $p = 0.02$), explained by a higher eye position for intermediate coherence compared to either zero coherence (mean difference: 0.05 dva, $T_{(13)} = 2.67$, $p = 0.02$) or high coherence conditions (mean difference: 0.08 dva, $T_{(13)} = 2.46$, $p = 0.03$), but importantly no main effect of choice ($F_{(1,13)} < 1$) and no interaction of choice and coherence ($F_{(3,39)} = 1.43$, $p = 0.25$). This means that any choice-specific results cannot be explained by differences in eye position.

Univariate fMRI results: motion coherence

Before the choice-decoding, we first investigated the univariate effect of motion coherence on *overall changes* in the amplitude of the BOLD signal to identify brain regions in which levels of activity

covaried with sensory evidence. Similar analyses have been reported in previous studies using "standard" sensorimotor choice designs (Heekeren et al., 2004, 2006; Ho et al., 2009; Kayser et al., 2010a, 2010b; Kovács et al., 2010; Tosoni et al., 2008). Since we were using a response-mapping screen that decoupled motor responses from decision-making we sought to confirm that our experiment was comparable to these previous studies. For that reason, we used a more lenient statistical threshold in this analysis than in later analyses ($T_{(21)}>4.49$, $p<0.0001$ uncorrected). Regions exhibiting a significant relationship between BOLD signal amplitude and motion coherence level are displayed in Fig. 2, red indicating a positive and blue a negative relationship. All results are reported in Table 1. We identified a number of regions with a *positive* relationship between BOLD signal amplitude and motion coherence, including bilateral angular gyrus, posterior cingulate cortex, superior frontal sulcus and ventro-medial prefrontal cortex. Among the brain regions exhibiting a *negative* relationship between BOLD signal amplitude and motion coherence were the frontal eye fields, the supplementary eye fields extending into the anterior cingulate cortex, the intraparietal sulcus and the anterior insula. Also early visual cortex showed this relationship, as well as a small cluster in left middle temporal cortex fully overlapping with MT+/V5 (see Table 1 for a complete list). No other region identified in this analysis overlapped with MT+/V5. The negative relationship between BOLD signal and stimulus strength may reflect increased top-down attention when the sensory evidence is weak (Ho et al., 2009; Kayser et al., 2010a, 2010b).

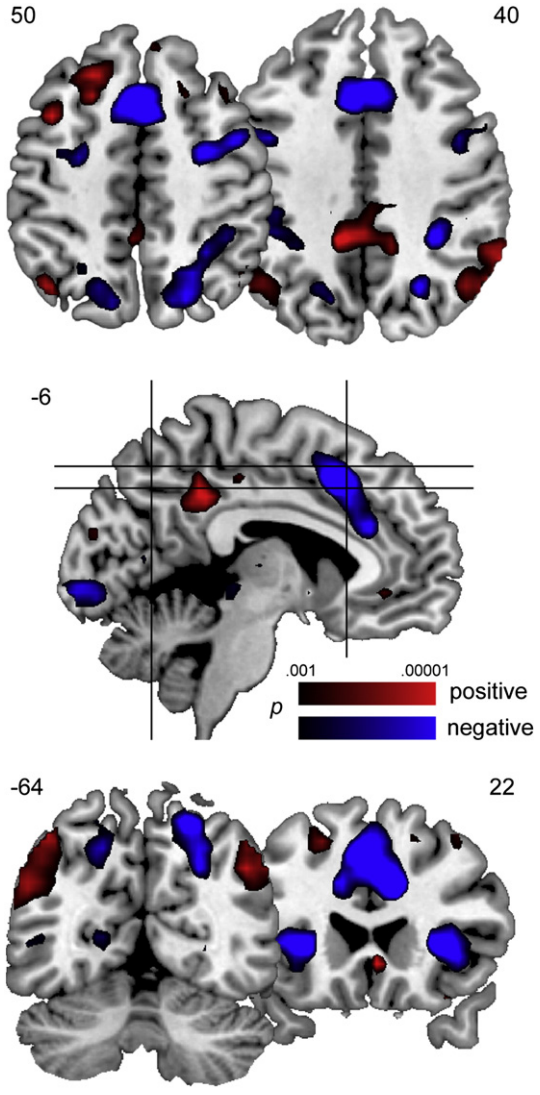

Fig. 2. Parametric univariate results. Results are indicated where the BOLD signal varied parametrically with the coherence of the stimuli. Red indicates a positive parametric response, while blue indicates a negative response. For illustrative purposes, *p*-values were scaled between 10^{-3} and 10^{-5} (uncorrected). Regions with a positive parametric response include left and right angular gyrus, posterior cingulate cortex and left superior frontal sulcus. A negative relationship was found in the frontal eye fields, supplementary eye fields and intraparietal sulcus, as well as anterior cingulate cortex, anterior insula, and other regions not shown here, but illustrated in Table 1. Also early visual cortex and left middle temporal cortex demonstrated a negative parametric response.

Table 1
Summary of parametric univariate results, separated for positive and negative parametric effects. Coordinates and T-values refer to the voxel with the highest T-value in each cluster, and the cluster size is defined by the number of significant voxels in each cluster ($p<0.0001$ uncorrected).

Region	X	Y	Z	T-value	Cluster size
Positive parametric effect					
Left angular/supramarginal gyrus	−54	−49	31	7.30	117
Posterior cingulate cortex	−12	−40	34	6.45	76
Ventro-medial prefrontal cortex	6	32	−5	6.17	15
Right angular/supramarginal gyrus	45	−61	37	5.85	97
Right putamen	18	8	−8	5.55	13
Left superior frontal sulcus	−21	29	49	5.49	20
Right middle/inferior temporal gyrus	63	−16	−8	5.38	18
Left superior parietal lobule	−42	−64	52	5.38	17
Left putamen	−21	5	−8	5.21	22
Right mid-cingulum	9	−22	46	5.19	11
Negative parametric effect					
Supplementary eye field/ACC	−6	17	43	9.61	397
Right frontal eye field	33	−1	61	9.58	164
Left anterior insula	−30	20	4	8.81	90
Right anterior insula	30	23	4	8.78	92
Right intraparietal sulcus	18	−64	58	7.79	155
Left frontal eye field	−30	−4	64	7.46	51
Early visual cortex	−12	−91	−11	7.41	185
Left mid-occipital gyrus	−30	−79	22	6.88	42
Left middle frontal gyrus	−33	53	13	6.28	24
Left middle temporal gyrus	−39	−58	10	6.24	17
Left inferior frontal gyrus	−45	2	31	5.77	30
Left intraparietal sulcus	−15	−70	43	5.41	14
Right thalamus	12	−10	4	5.38	13
Left inferior parietal lobule	−39	−40	43	5.11	10

Searchlight fMRI classification results: direction of motion

In the next step, we determined which brain regions carried information about the physical direction of motion of the stimulus. For linear motion, it has previously been demonstrated that motion directions could successfully be decoded from patterns of brain activity throughout early visual cortex and MT+/V5 (Kamitani and Tong, 2006; Serences and Boynton, 2007a, 2007b). However, these studies had used long blocks of stimulation, so it was not clear whether patterns of brain activity contained sufficient information to read out motion direction from patterns of brain activity using both low coherence levels and an event-related design with stimulus durations as short as 1.5 s.

A searchlight classification analysis was performed on each subject and each level of motion coherence to detect patterns of BOLD activity that carried information about upward vs. downward motion. As mentioned above, four classification brain volumes were available per subject (one for each level of stimulus coherence) that all were submitted to a group repeated-measures ANOVA. We looked for regions where at least one of the motion coherence levels was significantly different from chance ($F_{(4,63)}>8.83$, $p<0.00001$ uncorrected, $k=30$). This criterion was satisfied only in *early visual cortex* (Fig. 3), but did not extend to area MT+/V5. In early visual cortex, decoding accuracies increased across different levels of motion coherence ($F_{(3,63)}=8.84$, $p<0.0001$), while random motion led to chance

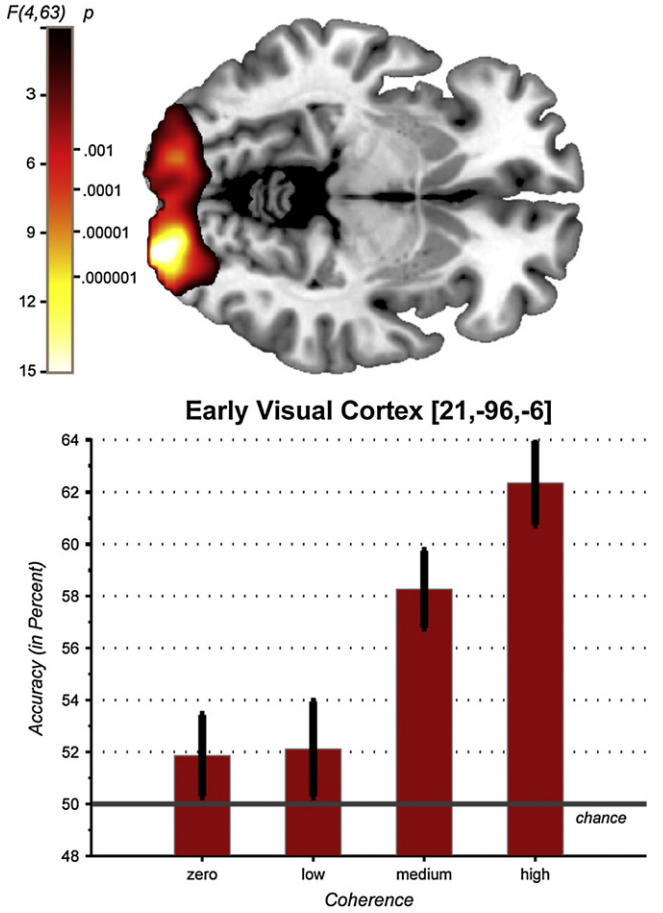

Fig. 3. Decoding the direction of motion. Using a searchlight classification analysis separately for each level of motion coherence, the motion direction of stimuli could be decoded only from early visual cortex. For illustrative purposes results were scaled between $p<10^{-4}$ (uncorrected) and the peak response. Decoding is strongest for the highest level of motion coherence and absent at the lowest level.

decoding (post-hoc t-test, $T_{(21)}=1.02$, $p>0.05$). In addition, we determined region MT+/V5 on the basis of a motion localizer and anatomical criteria (Dumoulin et al., 2000). We then performed a multivoxel pattern analysis only in this region of interest. We did find above-chance classification for left and right MT+/V5, but only at a lenient statistical criterion and only at the highest level of motion coherence ($T_{(21)}>1.72$, $p<0.05$). Please note that even our highest level of motion coherence will have yielded less discriminative stimulus information than in previous fMRI-decoding studies on motion coherence decoding (Kamitani and Tong, 2006). There was no overlap of results in early visual cortex with the MT+/V5 mask.

Searchlight fMRI classification results: perceptual choice

In a next step we identified brain regions carrying information about subjects' up vs. down *choices*, separately for each level of motion coherence. This searchlight analysis revealed which brain regions predicted perceptual choices, and how the choice-selective signals depended on the strength of sensory evidence. Please note that the motion direction of the physical stimulus and subjects' perceptual choices are more strongly correlated for higher than for lower coherence levels (higher accuracy, see Fig. 1b). Hence, lower coherence levels are better suited to identify neuronal signals that specifically encode the subjects' choices, rather than the stimulus (Britten et al., 1996).

Again, a searchlight analysis was performed on each subject, but this time we classified not motion directions, but the choices made by the subjects about the perceived motion direction, depending on the motion coherence. We looked for brain regions where at least one of the four conditions showed significantly above chance classification accuracies ($F_{(4,63)}>8.83$, $p<0.00001$ uncorrected, $k=30$).

Fig. 4 shows that two brain regions were identified using this procedure, namely *early visual cortex* and *left inferior parietal cortex* located in posterior parietal cortex around the angular gyrus. Early visual cortex showed an increase in decoding accuracies across different levels of motion coherence ($F_{(3,63)}=2.97$, $p<0.05$). This was expected, given the strong correlation between motion directions and choices at

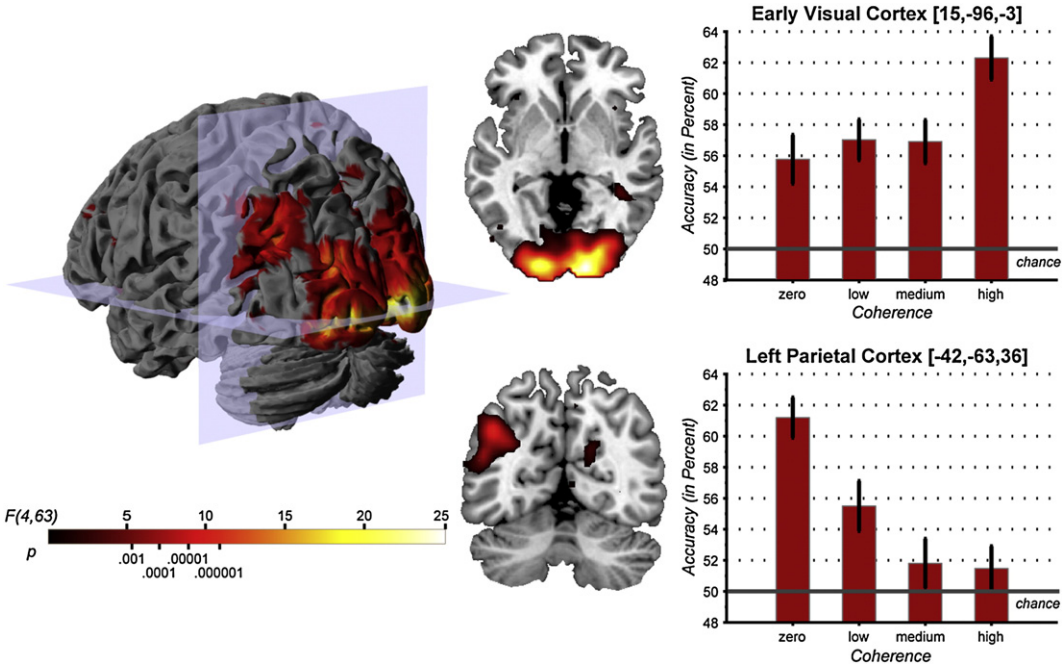

Fig. 4. Choice-selective signals in early visual and posterior parietal cortex. Two brain regions were identified that carried information about the subject's choice (up vs. down). Early visual cortex displayed an increase in decoding accuracies across levels of motion coherence. Even at the lowest level of coherence where the stimulus carried no predictive information, decisions could be decoded above chance. In left inferior parietal cortex decoding accuracies were highest for zero coherence and decreased with higher levels of motion coherence.

the highest level of motion coherence. However, even for the lowest level of motion coherence (where no net motion signal was presented to the subject), patterns of activity in visual cortex predicted decisions significantly above chance (post-hoc t-test, $T_{(21)}=3.64$, $p<0.001$). Decoding accuracies for decisions from an MT+/V5 region of interest showed a significant effect only at a lenient statistical criterion ($T_{(21)}>1.72$, $p<0.05$) and only for the highest level of motion coherence in left MT+/V5. Overlap with the MT+/V5 mask was 1.66% of voxels in the early visual cortex cluster, with a maximum of six subjects showing overlap in three of these voxels.

The results from the cluster in left inferior parietal cortex showed the reverse relationship: Here decoding accuracies were highest for the 'zero coherence' condition and decreased steadily for higher levels of motion coherence ($F_{(3,63)}=6.99$, $p<0.001$). At the highest level of motion coherence they were not significant (post-hoc t-test, $T_{(21)}=0.89$, $p>0.05$). This result shows that this posterior parietal region carried more predictive information about the decision when less sensory information was available to the observer. Overlap with the MT+/V5 mask was overall 8.83% of the cluster, and a maximum of three subjects showed overlap in two of those voxels.

To test whether the results could be explained by a larger overall BOLD response to one choice than another (e.g. a larger BOLD response to "up" than "down" choices), we carried out another mass-univariate GLM analysis as above, but this time modeling choices separately, effectively leading to 8 regressors (2 choices × 4 coherence levels). Using the same statistical threshold as for the multivariate searchlight analyses ($p<0.00001$ uncorrected, $k=30$), we found no discriminatory clusters that could separate up and down choices, demonstrating that the effects found in the classification analysis are not explained by overall changes in the BOLD signal amplitude.

Searchlight fMRI classification results: rule representation

Only at the time when a decision has been made and the response-mapping screen is shown, the subject can apply a response-mapping rule and execute a motor command to indicate their decision. In that way, our design allowed us to show choice-specific brain signals independent of the motor plan. This leaves open the question how the perceptual choice is translated into a motor response. The representation of the response-mapping rule is necessary to carry out this transformation of choice to motor response (Bode and Haynes, 2009).

To investigate this representation, we ran another searchlight classification analysis with the two different possible response-mapping screens (see Fig. 1c) as input to the classifier. The response-mapping screen should drive sensory responses to the stimuli on the screen in visual cortex (i.e. arrow up left – arrow down right, or vice versa) and induce a more abstract representation of the response-mapping rule in some higher-order brain regions (if up – press left, if down – press right, and vice versa). At the group level, a t-test was executed to detect brain regions that encode the response-mapping screen ($T_{(21)}>4.49$, $p<0.0001$ uncorrected). The results are shown in Fig. 5. Two sets of brain regions were found, one in bilateral early visual cortex (left: [−18, −97, −8]; right: [24, −97, 1]) likely reflecting the two different stimulus configurations, and another in bilateral dorsolateral prefrontal cortex (left: [−36, 32, 40]; right: [39, 35, 37]), likely reflecting abstract representations of the two alternative response-mapping rules.

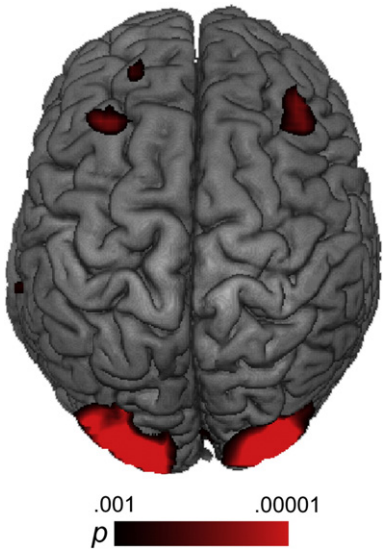

Fig. 5. Decoding of the response-mapping screen. Information about the response-mapping screen was found in early visual and dorsolateral prefrontal cortex. For illustrative purposes, p-values were scaled between 10^{-3} and 10^{-5} (uncorrected).

Discussion

In the vast majority of previous perceptual decision-making studies, decision processes had not been assessed independent of motor plans (Gold and Shadlen, 2007; Heekeren et al, 2008). These studies have used movement-selective neuronal signals in sensorimotor and motor brain areas as a proxy for tracking neuronal decision dynamics (Cisek and Kalaska, 2005; Donner et al., 2009; Horwitz and Newsome, 1999; Roitman and Shadlen, 2002; Salinas and Romo, 1998; Shadlen and Newsome, 2001; Tosoni et al., 2008). Their results have been central in linking neurophysiology to accumulator models of perceptual decisions (Ratcliff, 1978; Usher and McClelland, 2001). It has even been suggested that perceptual decision-making may be identical to motor intentions (O'Regan and Noë, 2001; Shadlen et al., 2008). Nevertheless, we can obviously make perceptual choices in a more abstract fashion, without directly transforming them into action plans.

Here, we used fMRI to determine where and how such abstract perceptual choices are encoded in the human brain when the decision process is decoupled from motor planning. We measured choice-selective brain signals across the human brain during a perceptual decision-making task in which choices were decoupled from motor plans. We found that both early visual and inferior parietal cortex carry information about the subjects' perceptual choices. The strength of this information, however, depended on the level of sensory evidence. Early visual cortex encoded the subject's decision even when there was no coherent motion, but carried more information when coherence was higher. In contrast, a region in left inferior parietal cortex carried most information about the choice of the subject at zero motion coherence, with a gradual decrease of information for higher motion coherence.

Our results indicate that both visual and parietal cortex are specifically involved in perceptual decision-making independent of motor plans. Interestingly, the amount of choice-selective information in both areas strongly depended on whether the sensory evidence was weak or strong, in an opposite manner. We found no single brain area in which the choice was encoded in a categorical, binary fashion throughout all visibility levels, i.e. independent of the amount of sensory evidence. Obviously, such a binary decision signal must arise somewhere in the nervous system when perceptual choices are directly mapped onto motor responses, because these motor responses are – by design – binary. By contrast, our present results suggest that when perceptual choices are *not* directly mapped onto motor responses, the brain may encode these abstract choices not in a binary manner, but rather as a graded variable, along with the associated certainty (Kiani and Shadlen, 2009).

Although the cortical signals we found were choice-selective, they do not necessarily directly contribute to the decision itself. For example, they may reflect selective feedback signals evolving as a consequence, rather than as the cause, of the decision (Nienborg and Cumming,

2009). While the exact nature of the involvement of parietal and visual cortex in this decision process awaits further study, importantly, the signals we identified in both regions cannot be explained by unspecific overall changes in activity during decision-making, because our analysis assessed the information about specific choices encoded in selective patterns of brain activity.

BOLD response amplitude increases with task demands

Previous fMRI studies of perceptual decision-making have found a number of brain regions in which the BOLD signal correlated with the decision of the subject (Bankó et al., 2011; Heekeren et al., 2004, 2006; Ho et al., 2009; Kayser et al., 2010a, 2010b; Kovács et al., 2010; Liu and Pleskac, 2011; Noppeney et al., 2010; Tosoni et al., 2008; Woolgar et al., 2011). In line with this work we found that decreases in the strength of sensory evidence were paralleled by increases in fMRI response amplitudes in a wide network of cortical regions outside of visual cortex. These regions include three areas known to be involved in "top-down" control of visual attention and visuo-motor processing (Corbetta and Shulman, 2002; Pessoa et al., 2003): the frontal eye fields, the supplementary eye fields, and the intraparietal sulcus. Also the anterior insula and the anterior cingulate cortex were found which have been related to categorization uncertainty (Grinband et al., 2006) and cognitive control (Ridderinkhof et al., 2004). Thus, the involvement of these brain regions in perceptual decision-making extends to situations in which stimulus and motor response are decoupled. This finding could indicate that subjects exert more top-down attentional control during perceptual decision-making in the face of weak sensory evidence, perhaps as a consequence of noticing difficulty of the decision (Philiastides and Sajda, 2006; but see Bankó et al., 2011). However, they could also reflect post-decisional processing, for example an increase in attentional control for the following trial (Botvinick et al., 2004; Miller and Cohen, 2001).

Choice-selective signals in early visual cortex

While our findings of overall BOLD signal changes are in line with those reported previously, such overall signal changes are difficult to interpret unambiguously, because they are not predictive of specific choices. In the present study we overcame this problem by directly characterizing choice-selective fMRI responses using multivariate decoding. One previous fMRI study used searchlight decoding to investigate changes in categorical representations of visual stimuli in human cortex during perceptual learning (Li et al., 2009). However, this study did not attempt to decouple the representation of perceptual choices from stimulus representations in the same task. For this, the most informative condition is zero stimulus strength (e.g., motion coherence), where choices and stimuli are uncorrelated and can thus be fully distinguished (Britten et al., 1996). Indeed, we observed that at zero motion coherence the outcome of the decision could be decoded from patterns of brain activity in early visual cortex.

Why was it possible to predict subjects' choices from patterns of brain activity as early as visual cortex, even when the stimulus contained no net motion? The choice-selective responses in early visual cortex may be driven by "bottom-up" (stimulus-dependent) factors, "top-down" (state-dependent) factors, or their interaction. It is possible that trial-by-trial fluctuations in the stochastic visual stimulus caused spurious direction-selective stimulus responses in visual cortex which subjects used for their choices in the "zero coherence" conditions (Britten et al., 1996). Even when no such bias exists in the physical stimulus, trial-by-trial fluctuations in spontaneous neural activity in sensory cortex may contribute to the contents of perception (Hesselmann et al., 2008a, 2008b; Wyart and Tallon-Baudry, 2009). Likewise, small and brief local changes in the salience of one motion direction – impossible to prevent in random dot motion stimuli – could lead to a selective neuronal response in visual cortex biasing perception to one direction of motion (Treue, 2003). In particular, it has been shown that choice-selective neuronal responses in visual cortex during perceptual choice tasks like ours may be caused by "top-down" signals selectively targeting those neurons that encode the evidence supporting the choice, and which arise during – or even after – decision formation (Nienborg and Cumming, 2009). It is, however, unknown how signals in V1 could participate in motion processing or in forming perceptual judgments.

We found no evidence for a similar effect in area MT+/V5 which is well known for processing motion directions (Born and Bradley, 2005; Zeki, 1974). This negative result is consistent with the fact that previous fMRI decoding studies found only small direction-selective effects in this region, even when using stimuli of maximum motion coherence and block designs (Kamitani and Tong, 2006; Serences and Boynton, 2007a), while our task was limited to much weaker stimuli and employed a less efficient event-related design. Under these circumstances it is possible that our decoding approach is not well suited for the size and structure of this brain region (Kamitani and Tong, 2006). A previous event-related fMRI study reported evidence for direction-selective responses even at zero coherence in MT+/V5 (Serences and Boynton, 2007b). However, in this study longer viewing durations and orthogonal motion directions were used which may yield different results than the short viewing durations and collinear motion directions typically used in perceptual decision-making studies. In particular, orthogonal motion directions maximize the possibility that a classifier could pick up motion streaks (Apthorp, 2010, pp. 140–144). These perceived oriented lines along the path of motion could be classified when motion directions are orthogonal, but not when they are collinear, because in that case streaks have the same orientation independent of the direction of motion. While this is less of a problem for the zero coherence condition, viewing durations of 12 s and the expectation of no change in visual stimulation could lead to strong choice-specific top-down signals in area MT+/V5 (Kayser et al., 2010a, 2010b) that could possibly be picked up by a classifier.

Choice-selective signals in posterior parietal cortex

In addition to visual cortical areas a region in left posterior parietal association cortex carried information about the decision. This region was located around the angular gyrus and does not belong to the typical sensorimotor association regions reported in studies of perceptual decision-making (Tosoni et al., 2008) which lie more medial and superior, including eye-movement and reach-selective regions around the intraparietal sulcus (Culham et al., 2006; Silver and Kastner, 2009; Swisher et al., 2007). Instead, our results point towards a role of this region in decision-making when decisions need to be encoded in an abstract form.

The posterior parietal region we identified was maximally predictive of the subjects' decision at zero motion coherence, with a gradual decrease of decoding accuracies for higher levels of motion coherence. Is it possible that subjects accumulate sensory information from visual cortex only when the evidence is low? In this scenario, accumulation would not be necessary for strong evidence, so that subjects could read out instantaneous sensory responses (Uchida et al., 2006), in our case from visual cortex. However, such a pattern of results is not consistent with previous work, and it would not be explained from the different functions relating spike rates to accumulation of sensory evidence at different levels stimulus visibility. For fixed stimulus durations (as in our case), the choice-selective brain activity should increase with motion coherence when integrated across the whole stimulus interval (Heekeren et al., 2004; Mazurek et al., 2003; Shadlen and Newsome, 2001). This result suggests that different or additional processes contributed to the outcome of the decision in the face of low sensory evidence.

Another possibility is that the response reflects the subjects' criterion which would dominate the outcome of decisions when evidence is weak. This criterion could be governed by a subject's internal "hypothesis" about the direction of motion (Friston, 2005), but also a passively fluctuating bias signal which is most informative when the motion coherence is high, but which influences the decision when sensory evidence is low (Shadlen and Newsome, 2001). Either way, the results are in line with the notion that decisions are governed by different signals when making decisions at low and high sensory evidence. We do not exclude the possibility that the signal in other high-level regions followed the decision of the subject, but that our method was not sensitive enough to pick up these effects. What our results do show is that this parietal region is the one *most strongly* involved in decisions at low levels of sensory evidence.

Relationship between mean BOLD signal effects and searchlight decoding results

It is interesting to note that we did not find any brain region where the BOLD signal increased together with the amount of information available to the classifier. If any overlap was present, the BOLD signal went in the opposite direction of the decoding accuracies when motion coherence was varied. This result suggests that the increase in mean BOLD signal in a brain region can be decoupled from the spatial patterns encoding specific neural responses. Similar counterintuitive findings have been reported previously. For example, it has been shown that the BOLD signal in area MT+/V5 which is well known to encode motion speed and direction (Born and Bradley, 2005; Zeki, 1974) can increase with decreasing motion coherence (Kayser et al., 2010a, 2010b), and that this effect is related to increasing top-down attention with decreasing motion coherences (Kayser et al., 2010b). We replicated this finding for area MT+/V5 and extended it to early visual cortex. Probably, this top-down effect is stronger than the bottom-up increase in neural activity through higher motion coherence, leading to overall decreases in BOLD signal with increasing motion coherence. Similarly, many of the mean BOLD signal variations reported in the present study may be related to such attentional or performance monitoring effects (Botvinick et al., 2004; Corbetta and Shulman, 2002; Miller and Cohen, 2001; Pessoa et al., 2003; Ridderinkhof et al., 2004). Pattern classifiers can pick up weak choice-specific signals that may not become apparent in the mean BOLD signal response (Li et al., 2009) and which may co-occur together with such top-down signals.

In a similar vein, the BOLD responses in the parietal region overlap with a brain region that typically deactivates during the task (Singh and Fawcett, 2008). In our case, this brain region is deactivated less with increasing motion coherence. This could mean one of three things: First, activity in this brain region is driven only by the difficulty of the task. In that case deactivation is stronger with lower motion coherences, because the task becomes more difficult and all resting-state activity needs to be suppressed to focus on the task. Second, there is a task-negative response and on top of that an increase in activity which overlaps with the overall task-specific deactivation and which increases with motion coherence. Clearly, this region of the posterior parietal cortex serves other processes than only to deactivate during the task (Dehaene et al., 1999; Price, 2000), so this scenario is a valid possibility. Third, the brain could in principle prepare several responses in another brain region, but only execute them as soon as sufficient information has been accumulated. Selective deactivation in posterior parietal cortex could in that case prevent overly fast responses in the brain regions encoding the response. While we cannot directly discriminate between these three scenarios, our results demonstrate choice-specific brain signals from the posterior parietal cortex and in that way argue in favor of the second alternative, i.e. separate but overlapping responses to different aspects of the task. Taken together, a negative BOLD response alone does not seem to justify the exclusion of brain regions as candidates for decision-making regions (Ho et al., 2009; Kayser et al., 2010a, 2010b; Tosoni et al., 2008).

Choice selectivity vs. motor planning

Given our design of decorrelating perceptual choice ("up" vs. "down") and motor responses (left- vs. right-hand button press) on a trial-by-trial basis, we are confident that cortical responses specifically encoding perceptual choices found in our analysis are not confounded by cortical responses encoding motor plans. However, it is possible that our present design missed some choice-selective responses that co-existed with response-selective signals in a given brain region. Neuronal signals that carry information both about the perceptual choice and the motor plan have been found to co-exist in macaque LIP in the case of saccadic responses (Bennur and Gold, 2011). In our present design, the BOLD responses to both signals will overlap in time. Thus, in such regions it may be difficult to pull apart specific patterns of brain activity selective for the choice or the motor response, possibly yielding a null result. In principle, it would be possible to fully separate these signals by longer and jittered delays between stimulus, response-mapping screen, and motor response. However, we chose not to use such an approach, because this would have strongly reduced the efficiency of our design. In addition, even delays of a few seconds before responding could have lead to effector-independent re-coding of information in memory-related brain regions, which would be difficult to relate to decision-making signals without such re-coding. Other studies using time jitter thus may detect additional brain regions encoding perceptual choices, possibly including the human homologue of area LIP (Bennur and Gold, 2011) which should lie anterior of the parietal region identified in the present study.

The present design may not eliminate motor planning altogether. It is possible that subjects prepared both left- and right-hand responses during the decision formation, irrespective of the choice, and then only selected the appropriate response after the presentation of the response-mapping screen, effectively suppressing motor preparation of one while maintaining motor preparation of the other hand. While subjects may have carried out such motor planning, the selective motor preparation signal should be reflected in the motor response component, because it predicts the motor response of the subject. Given that we effectively decorrelated motor responses and perceptual choices, our results thus cannot be explained by motor preparation, even if the subject chose to prepare all possible motor responses. However, our design did not prevent subjects to carry out such motor preparation. This process could, however, not be captured with the present design, because motor preparation and execution are impossible to separate in our task. Taken together, our analyses preclude any signals to be picked up that were confounded by motor preparation.

Previous studies on the encoding of abstract choices

Previous monkey electrophysiology studies have demonstrated signals reflecting abstract choices in the superior colliculus, supplementary eye field (Horwitz et al., 2004), and the lateral intraparietal area (Bennur and Gold, 2011). Although choices can accurately be predicted from neuronal responses in the frontal eye field (Kim and Shadlen, 1999), this region only seems to be involved in the decision process when a motor response (saccade) is planned concomitantly (Gold and Shadlen, 2000, 2003). In humans, it is still a matter of debate how abstract decisions are encoded. One approach has been to detect brain signals that are invariant to the motor effector used to carry out the task, and while some studies reported brain regions responding irrespective of the response modality (Heekeren et al., 2006; Ho et al., 2009; Liu and Pleskac, 2011), others could not find modality-independent evidence (Tosoni et al., 2008). More specifically, Heekeren et al. (2006) found the left superior frontal sulcus to

respond irrespective of motor effector, Ho et al. (2009) found signatures of evidence accumulation in the right anterior insula also irrespective of motor effector, and Liu and Pleskac (2011) found the posterior intraparietal sulcus, precentral sulcus and anterior insula to respond both independent of motor effector and of foreknowledge of which effector to use. While we also detected those regions with the same direction of BOLD signal modulation, we found no evidence for their involvement in representing the particular choice of subjects. These conflicting findings could thus be resolved if one assumes that those signals were in fact not encoding the choice of the subject, but reflected rather unspecific albeit possibly decision-making related changes in the overall level of brain activity with sensory evidence.

Summary

Our results show how perceptual choices are encoded in the human brain when motor planning can be performed only after accumulation of sensory evidence. While many brain regions exhibited strong correlations between BOLD signal response amplitude and sensory evidence, we showed that these responses are not sufficient to qualify as selective for perceptual choice, a hallmark for "decision-related" activity in single-cell recording studies (Gold and Shadlen, 2007). By classifying perceptual choices independent of motor plans, we showed that both early and left posterior parietal cortex contribute to the perceptual decision, albeit to different degrees depending on sensory evidence: Visual cortex encoded choices already when no discriminatory information was present. With increasing motion coherence information in early visual cortex increased, while it decreased in posterior parietal cortex. When choices are encoded in an abstract format, dorsolateral prefrontal cortex may be involved in mapping this information to specific motor responses (Sakai and Passingham, 2006). To conclude, our results directly link patterns of brain activity to the representation of abstract perceptual choices in the human brain.

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