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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