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Similar neural mechanisms for perceptual guesses and free decisions

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ABSTRACT

When facing perceptual choices under challenging conditions we might believe to be purely guessing. But which brain regions determine the outcome of our guesses? One possibility is that higher-level, domain-general brain regions might help break the symmetry between equal-appearing choices. Here we directly investigated whether perceptual guesses share brain networks with other types of free decisions. We trained an fMRI-based pattern classifier to distinguish between two *perceptual* guesses and tested whether it was able to predict the outcome of similar *non-perceptual* choices, as in conventional free choice tasks. Activation patterns in the medial posterior parietal cortex cross-predicted free decisions from perceptual guesses and vice versa. This inter-changeability strongly speaks for a similar neural code for both types of decisions. The posterior parietal cortex might be part of a domain-general system that helps resolve decision conflicts when no choice option is more or less likely or valuable, thus preventing behavioural stalemate.

Introduction

Perceptual decision-making is essential for our every-day life and seems to happen effortlessly when sufficient sensory information is available. Perceptual decision-making under varying sensory conditions has been intensively studied using single-cell recordings in monkeys (Britten et al., 1996; Gold and Shadlen, 2007; Shadlen and Newsome, 2001) and functional magnetic resonance imaging (fMRI) and electroencephalography (EEG) in humans (Heekeren et al., 2004, 2008; McKeeff and Tong, 2007; Philiastides and Sajda, 2006, 2007; Serences and Boynton, 2007). One challenging question, however, is how we make decisions in the absence of sufficient information when stimuli are very difficult to see. This problem is exacerbated by the absence of "priors" in many perceptual tasks, where choice alternatives are equally likely and rewarding. Participants are thus frequently faced with a 'symmetry situation': How do we decide between equal options without getting stuck like Buridan's mythical donkey, starving in the middle between two haystacks? One possibility is that we rely on the same sensory neural systems as for veridical perception but that random noise fluctuations in the sensory system determine trial-by-trial choices (Shadlen et al., 1996; Swets, 1961). Another possibility is that domain-general regions are used to break the symmetry between equal options (Deco and Romo, 2008).

Using fMRI in combination with pattern classification techniques (Haynes and Rees, 2006; Norman et al., 2006) we recently assessed which brain regions predict perceptual choices under high and low visibility. We found that under *low* visibility, perceptual choices about objects could be decoded from medial posterior parietal cortex, but not from sensory brain regions (Bode et al., 2012). This parietal region was clearly distinct from sensory areas in the lateral-occipital complex (LOC) in ventral visual cortex, which encoded sensory information about object categories (Haxby et al., 2001; Williams et al., 2007). The medial parietal area strongly overlapped with a network that was recently found to be involved in free decision-making (Soon et al., 2008). Thus, we reasoned that guessing and free decisions might share similar brain networks, a hypothesis that is yet to be tested.

Here, we conducted an event-related fMRI study in which participants made category choices about pianos and chairs using three different conditions. In all conditions participants saw brief, repeated mask–target–mask sequences. (1) Perceptual choices under high visibility: On each trial the sequence contained an object image (piano or chair) that was clearly visible. Participants were asked to identify the category of the presented object. (2) Perceptual choices

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under "low visibility" (perceptual guesses): Participants were given the same task but the timing of the stimuli was chosen to yield strong masking and the sequence only contained a neutral noise image instead of an object. The participants were unaware of this manipulation (as confirmed with post-experimental questionnaires and interviews) and thus believed to be making normal (albeit difficult) perceptual guesses. Thus, this condition was in fact a zero-visibility condition. (3) Free choices: The presentation was identical to the "low visibility" condition, again ensuring that no visual bias could drive the decisions. Participants were asked to spontaneously and freely choose either "piano" or "chair", whatever category came first to their minds. They were instructed to ignore the visual stimulus display (even though it did not contain any differential visual information). We then used a "searchlight" decoding approach (Haynes et al., 2007; Kriegeskorte et al., 2006) to search for brain regions that encoded participants' category choices in all three conditions. In order to identify potential neural representations of the choices, we identified regions that exhibit different response patterns to the different choice options. This classification-based approach is frequently used in order to identify information-coding neural response patterns. The crucial analysis used activation patterns associated with decision outcomes from perceptual guessing to cross-predict free decisions, and vice versa. This analysis aimed to search for any brain region in which the choice-predictive activation patterns were *interchangeable* between the two conditions. Finding such a brain region would not provide conclusive evidence for a shared neural code for both decisions, as also non-decision related processes could systematically differ between the choice options. It would be a strong indicator, however, that such pattern similarity may reflect important similarities in decision-making.

Material and methods

Participants

Sixteen right-handed participants with normal or corrected to normal visual acuity gave written informed consent and participated in the study. The experiment was approved by the local ethics committee and was conducted according to the Declaration of Helsinki. One participant indicated that he had noticed the missing object images and was excluded. The data from the remaining 15 participants (7 female; mean age 25 years; range 21–28) were used for the analyses.

Stimuli and experimental procedure

The stimuli were 24 pictures of pianos and chairs, created from freely available pictures from the Internet or custom-made photographs, showing objects in different natural backgrounds (Bode et al., 2012; Grill-Spector et al., 2000). Pictures were transformed into grey-scale versions with a size of 400×400 pixels and were presented on a grey background. Two different scrambled masks (pre- and post-mask) were used during presentation. Masks consisted of 10×10 squares from random object pictures, each 40×40 pixels, rearranged such that they did not contain any identifiable parts of objects. The visual angle was 7.15° (stimuli and masks). For the invisibility condition, one noise image was used that consisted of scrambled phase textures. To create this, a two-dimensional Fourier transformation was performed on one of the masks. The phase map was scrambled by adding a random value of $+/-1.75^{*}\Pi$ to each phase angle (Malach et al., 1995). The resulting phase maps were then transformed back to an image and contrast-normalized. Note that all noise trials used the same noise stimulus to avoid biasing participants' choices by incidental variations in similarity to an object category.

Each trial consisted of a brief "standing wave" of the same mask–target–mask sequence (Bode et al., 2012) repeated three times, with a white fixation cross centrally superimposed. A combination of forward- and backward-masking was applied. For the high visibility condition, on each trial one object image was shown, preceded by a 150 ms pre-mask, then presented for 66.7 ms, and followed by a post-mask (500 ms minus target duration = 433.3 ms). For the perceptual guessing condition, only the noise image was shown, also preceded by a 150 ms pre-mask, then presented for 16.7 ms, and followed by a post-mask (500 ms minus target duration = 483.3 ms) (Fig. 1).

The experiment implemented three conditions (equal number of trials per condition in each run). The first two conditions required the participants to categorize either the highly visible objects (high visibility condition, HVC) or objects they believed to be poorly visible (perceptual guessing condition, PGC). The third condition was a free decision condition (FDC) for the same two categories. No feedback was given during the experiment. The task was indicated by the colour of the fixation cross in the beginning of each trial (red = categorization; green = free decision; duration 750 ms). For the HVC, on each trial one object stimulus (piano or chair) was shown. For the PGC participants were told that an object stimulus was presented, albeit that it was sometimes difficult to detect. However, only the strongly masked noise image was presented which created the strong impression that there was indeed an object presented without revealing its identity. For the FDC, participants were presented with the same stimulus sequence as for the PGC but they were instructed to spontaneously choose the category that first came to their mind, independent of the presentation. It was pointed out that they should choose an *object category* instead of a response button and not change their mind after making a decision. Participants were also asked to always make a decision, even if uncertain. The use of noise stimuli guaranteed that participants' decisions were pure guesses or free choices (for pianos or chairs), without residual visibility influencing either process. Participants indicated their choice by pressing one of two response buttons (right index- and middle finger), pseudo-randomized presented on either side of the fixation cross (2000 ms). This manipulation allowed the de-correlation of motor responses and category choices. It was followed by a jittered fixation period (7 s, 8 s or 9 s). Participants performed six runs (72 trials per run). The same object image was never shown twice in one run. The order of object images was individually randomized for each participant and each run. Adherence to the task instructions and success of the experimental manipulation were assessed after the experiment using a questionnaire (for results see Fig. 2).

fMRI data acquisition

Functional MRI volumes of the whole brain were acquired using a Siemens TRIO 3 T scanner (Erlangen, Germany) with a standard head coil (42 axial slices, TR = 2800 ms, echo time TE = 30 ms, resolution $3\times3\times2$ mm^3 with 1 mm gap). Within each of the six runs, 208 volumes were acquired for each participant using gradient-echo EPI. The first two volumes of every scan were discarded by default to allow for magnetic saturation effects.

fMRI data analyses

First, we performed pattern classification analyses (Haynes and Rees, 2006; Mur et al., 2009; Norman et al., 2006; Pereira et al., 2009) in order to identify brain regions encoding information about category choices within each decision condition separately. Because the PGC and FDC were unconstrained by the stimulus and participants were free to make either choice, the data of 8 runs had to be excluded from the analyses for these conditions because they