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Varieties of perceptual instability and their neural correlates

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ABSTRACT

We report experiments designed to learn whether different kinds of perceptually unstable visual images engage different neural mechanisms. 21 subjects viewed two types of bi-stable images while we scanned the activity in their brains with functional magnetic resonance imaging (fMRI); in one (intra-categorical type) the two percepts remained within the same category (e.g. face–face) while in the other (cross-categorical type) they crossed categorical boundaries (e.g. face–body). The results showed that cross- and intra-categorical reversals share a common reversal-related neural circuitry, which includes fronto-parietal cortex and primary visual cortex (area V1). Cross-categorical reversals alone engaged additional areas, notably anterior cingulate cortex and superior temporal gyrus, which have been posited to be involved in conflict resolution.

Introduction

In trying to obtain knowledge about the external world, the brain employs two strategies; one consists of stabilizing the world by discarding all the superfluous and inconstant changes, one example of which is the generation of constant colours, which makes the brain independent of the continual changes in wavelength-energy composition of the light reflected from objects and surfaces (Land, 1974; Zeki, 1980), thus giving us knowledge about them through their colour. But there are also stimuli whose configuration is such that they are sources of uncertain knowledge since they remain open to more than one interpretation, classic examples being the Necker Cube and the Rubin Vase. To allow for the uncertain knowledge derived from such perceptually unstable stimuli, the brain appears to have evolved another strategy — a system that is stable in its instability, in the sense that it can allow for more than one interpretation of a stimulus even when higher cognitive factors impel the interpretation in one direction (Zeki, 2008). This phenomenon has been especially useful in investigating neural systems that correlate with the conscious perception of objects and previous neuroimaging studies have shown that frontal and parietal cortex and functionally specialized visual areas are engaged in all perceptual reversals (e.g. Andrews and Schluppeck, 2004; Kanai et al., 2010; Kleinschmidt et al., 1998; Lumer et al., 1998).

Bi-stable figures can be divided broadly into two sub-types, those showing *intra-categorical* and those showing *cross-categorical* reversals. The Necker cube belongs to the former: it is perceived as one object (category) that can be in one of two recessional states. The Rubin vase belongs to the cross-categorical variety, in that it can alternate perceptually between two categories (face and vase). In both, there is an *obligate bi-stability* (and an obligate multi-stability in others) since it is difficult, if not impossible, to prevent the transition from one state to the other; both are perceptually “correct” at any given moment and each occupies sovereignly the conscious perceptual stage for a given moment before the other interpretation replaces it to supervene. This makes it especially interesting to compare the brain activity produced by the two types of bi-stability. The cross-categorical transition results in a conflict condition since the perceptual transition is between two different categories; by contrast, the transition in intra-categorical examples is only a change from one state to another of the same category (object) and hence introduces no categorical conflict in what the image is, but only in its configuration. In this study, we therefore wanted to learn whether the same neural circuits are engaged in the two kinds of bi-stability. Our working hypothesis was that intra-categorical and cross-categorical bi-stability will both engage the same fronto-parietal areas but that the cross-categorical bi-stability will engage cortical areas that have been shown to be prominently engaged in conflict resolution, principally the anterior cingulate cortex (ACC). We hypothesized further that activity in the ACC would be restricted to the reversal phase of the unstable images, since it is then alone that a conflict arises about the knowledge derived from the stimulus. Hence our study was specifically focused on the engagement of the ACC in the two kinds of obligate bi-stability, to learn whether activity in it would allow us to distinguish neurologically between the two kinds of perceptual transition.

To do so, we used functional magnetic resonance imaging (fMRI) to scan brain activity when subjects viewed both types of bi-stable figures and indicated when their percepts alternated between two interpretations; this allowed us to distinguish between activity that correlates with the reported perceptual reversal for both types of stimuli.

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Materials and methods

Subjects

21 healthy right-handed volunteers (9 male, 12 female, mean age 23.7 years) participated. All had normal or corrected-to-normal vision, and none had a history of neurological or psychiatric disorder. Written informed consent was obtained from all. The study was approved by the Ethics Committee of University College London and conforms with the Code of Ethics of the World Medical Association (Declaration of Helsinki; printed in the British Medical Journal 18 July 1964). All data was anonymized.

Procedure

Subjects were instructed to report repetitively their perception of visual stimuli during stimulus presentation and to press one of two buttons with their right hand to indicate one or the other of the two possible directions of perceptual transitions. After reporting a transition, they kept the key pressed while the ensuing percept was stable. We calculated middle-points for each time-interval between each button press and release (that is, during the period when subjects' perception was stable) and used these as the onsets for stable perception in an event-related analysis (Kleinschmidt et al., 1998). Subjects' reports thus defined the occurrence of perceptual reversals and the presence of stable perceptions. There were, therefore, two critical time-points, when a reversal occurred and when perception was stable.

We used a variety of bi-stable figures belonging to two classes of stimuli: in one class (cross-categorical) were stimuli for which perception alternates between one category and another (e.g. between a face and a body or a vase and faces, see Fig. 1) while in the other (intra-categorical) class were stimuli in which the transition is between two percepts belonging to the same category (e.g. from one face to another, see Fig. 1). Table 1 provides all stimulus categories used in the experiment. Preceding the fMRI experiments, participants viewed all bi-stable figures and familiarised themselves with the stimuli. At the beginning of each trial in the scanning sessions, subjects were informed what stimulus categories would appear in the coming trial, with an instruction for which button to press to indicate their percepts (e.g. "*Face = left button, Body = right button*"). The stimuli covered approximately 8° × 8° of the visual field and included a central fixation cross. Inter-reversal time-spans can be controlled with parameters that depend on stimulus type, visual field coverage and fixation point (Borsellino et al., 1982; Kleinschmidt et al., 1998). These stimulus settings followed a previous study using bi-stable figures (Kleinschmidt et al., 1998). All stimuli were grey-scaled pictures and the brightness of each was adjusted to the averaged brightness of all. Stimulus presentation lasted for 60 s followed by a 20 s fixation period during which the fixation cross was presented on a black background. Subjects were instructed to fixate the cross throughout scanning. There were 8 stimuli for each reversal condition, resulting in 16 experimental stimuli in total. The experiment consisted of 4 scanning sessions and each session had 4 stimuli. The order of the stimulus presentation and button-pressing were counterbalanced across subjects. Number of reversals and

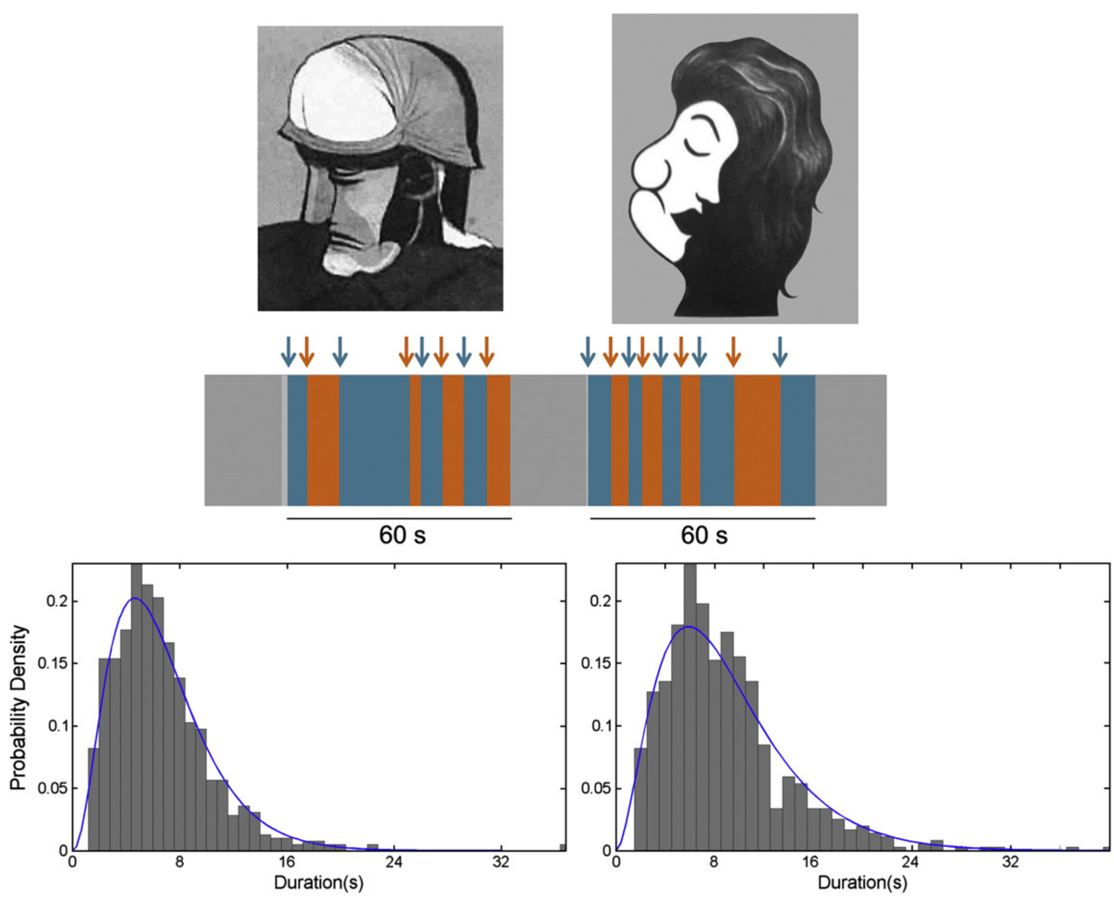

Fig. 1. Upper panel: examples of bi-stable figures used in the experiment. To the left, a *face–body* bi-stabile figure is an example of cross-categorical reversal, and to the right, a *face–face* bi-stabile figure is one for intra-categorical reversal. Middle panel: illustrative example of responses while viewing a bi-stable stimulus, derived from one subject's data. Blue phases correspond to one percept and orange ones to another. Lower panel: the distributions of grand averaged inter-reversal times (durations of percepts) reported by participants. The blue lines show the fitted gamma distribution.