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The human amygdala encodes value and space during decision making

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ABSTRACT

Valuable stimuli are invariably localized in space. While our knowledge regarding the neural networks supporting value assignment and comparisons is considerable, we lack a basic understanding of how the human brain integrates motivational and spatial information. The amygdala is a key structure for learning and maintaining the value of sensory stimuli and a recent non-human primate study provided initial evidence that it also acts to integrate value with spatial location, a question we address here in a human setting. We measured haemodynamic responses (fMRI) in amygdala while manipulating the value and spatial configuration of stimuli in a simple stimulus–reward task. Subjects responded significantly faster and showed greater amygdala activation when a reward was dependent on a spatial specific response, compared to when a reward required less spatial specificity. Supplemental analysis supported this spatial specificity by demonstrating that the pattern of amygdala activity varied based on whether subjects responded to a motivational target presented in the ipsilateral or contralateral visual space. Our data show that the human amygdala integrates information about space and value, an integration of likely importance for assigning cognitive resources towards highly valuable stimuli in our environment.

Introduction

Fundamental for approach and avoidance behaviour is the need to localize value in space. The amygdala is a structure widely implicated in encoding the value of stimuli (Jenison et al., 2011; Morrison and Salzman, 2010; Paton et al., 2006). Electrophysiological recordings in nonhuman primates show how the amygdala contains neurons with sustained preferences for positive or negative affective value, a value signal that is also related to the animal's approach or avoidance behaviour (Paton et al., 2006). Though such influence on behaviour could be the result of a general arousal state mediated by the amygdala (Davis and Whalen, 2001), this is contradicted by demonstration of amygdala activity linking spatial and motivational representations (Peck et al., 2013).

Amygdala is not the only brain region involved in assigning and updating stimulus value. A growing literature provides a complex picture of brain regions that contribute to value encoding (Clithero and Rangel, 2013; Rangel and Hare, 2010) and several of these brain areas also serve other cognitive and emotional functions (Barrett and Satpute, 2013). However, in order to act upon valuable stimuli, it is essential to localize them in space. While regions such as orbitofrontal cortex (OFC) and ventral striatum both carry value related signals (Kable and Glimcher, 2009), it is also the case that they show low or even absent spatial selectivity (Lansink et al., 2012; Padoa-Schioppa and Assad, 2006). Interestingly, both of these regions share close anatomical connections with the amygdala (Haber and Knutson, 2010), with dynamic and complex relationships between these areas characterizing a range of value-guided decisions and behaviours (Barberini et al., 2012; Morrison et al., 2011).

The integration of stimulus value with its spatial configuration in the human amygdala remains little investigated. While functional neuroimaging studies (Basten et al., 2010; De Martino et al., 2006; Gottfried et al., 2003; Ousdal et al., 2012) and electrophysiological recordings (Belova et al., 2008; Paton et al., 2006; Schoenbaum et al., 2003) implicate the amygdala in encoding the value of stimuli, there has been little exploration of whether it is important for localizing motivational stimuli in space. It is of interest that patients with isolated amygdala lesions do support sensitivity to spatial information. For instance, patient SM who has bilateral amygdala lesions and difficulties recognizing fearful facial

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expressions, shows a resolution of this deficit when her attention is directed towards the informative eye region of the faces, suggesting a spatial attention aspect to her deficit (Adolphs et al., 2005). Moreover, humans detect emotional images or words faster than their neutral counterparts (Anderson, 2005; Eastwood et al., 2001; Fox, 2002), and locations previously associated with highly valuable events interfere with the search for present targets (Anderson et al., 2011). In addition, though many studies report amygdala activity in response to passive obtainment of rewards, active responding for a reward in space appears to yield significantly greater BOLD amygdala response then is the case for passive receipt (Elliott et al., 2004).

If indeed information about stimulus' value and its spatial location converge in the human amygdala, then this begs questions as to the origin of the spatial information. Both the dorsal visual stream (Ungerleider and Haxby, 1994) and the lateral (i.e. ventrolateral and dorsolateral) prefrontal cortex (Corbetta and Shulman, 2002) contain neurons sensitive to object localisation. However, both of these brain areas have few connections to the amygdala (Freese and Amaral, 2009). Another possibility is that the dorsal anterior cingulate cortex (dACC), which conjointly encodes spatial attention and reward value (Kaping et al., 2011), and shares bilateral connections with the amygdala (Beckmann et al., 2009; Ghashghaei et al., 2007), might provide the necessary spatial information.

We investigated the spatial sensitivity of a value signal in amygdala during a simple stimulus–reward task in which outcome value and the motor response requirements were kept constant, while the spatial specificity of the reward varied. We hypothesized that amygdala would encode value in space, with the greatest activity manifest when these two stimulus' attributes had to be integrated in order for optimal decisions. Furthermore, to address the question of access to spatial information by the amygdala we tested whether the functional association between amygdala and dACC varied according to the spatial representation of a rewarding event.

Materials and methods

Subjects

Eighteen healthy subjects (mean age ± SD = 25 ± 6 years; 9 women) were included in the study after giving written informed consent. The study was approved by the Norwegian Regional Committees for Medical and Health Research Ethics. Prior to participation, subjects were screened to exclude somatic and psychiatric illness, substance abuse and MRI-incompatibility. All subjects received 300 Norwegian Kroner (kr) (150 kr for a screening interview and 150 kr for the fMRI session) for their participation and kept additional money won in the experiment described below.

fMRI paradigm

We created a new paradigm using visual numbers presented pairwise in an event-related design. Each trial consisted of a number pair presented for 800 ms, and subjects had to make their response while the numbers were presented on the screen. Trials that did not have a response within 800 ms were coded as "missed responses". The order of trial presentation was randomized across subjects. Trials were separated by a jittered inter-trial interval lasting 5 ± 2 s. For each trial, purple numbers were presented in pairs on a black background. The numbers occurred horizontally to each other and were either similar or different in magnitude. The number value corresponded to an amount a subject could win in Norwegian Kroner (kr; 1 kr equals approx. 0.17 USD), and was either 0, 2 or 4 kr (see Fig. 1). The task for subjects was to press a response button corresponding to the amount of kr the subject wanted to obtain, which under the assumption that they wanted to maximise their gains corresponded to the highest number. Subjects were given verbal instructions prior to scanning and also performed a practice version of the task. During the practice, subjects completed one trial of each condition, and thus familiarized themselves with the visual appearance of the stimuli and the time limits for responding. Before the practice, subjects were told that they were free to respond however they preferred, but that one response should be given for each trial. The combination of two similar numbers (i.e. 2–2 or 4–4), called the non-spatial value condition, had no preferred response. In the spatial value condition the numbers differed, and one response was more rewarding than the other (the one with the highest number). The number pairs in spatial value trials always consisted of a zero paired with a valuable stimulus (i.e. 4–0 or 2–0). The 0–0 condition provided a baseline. By creating these five conditions, we could independently manipulate reward magnitude and spatial specificity. We hypothesised that amygdala would activate more in trials requiring greater spatial specificity for reward obtainment than trials with less necessity for localisation, despite equal outcome values. The use of hands was counterbalanced. Subjects were told that they could keep all the money earned in the experiment, but they would not receive any feedback during the task indicating the outcome of the trail or their overall earnings. Twenty trials of each condition were presented, with the total scan time lasting 12.2 min. The paradigm rationale is displayed in Fig. 1.

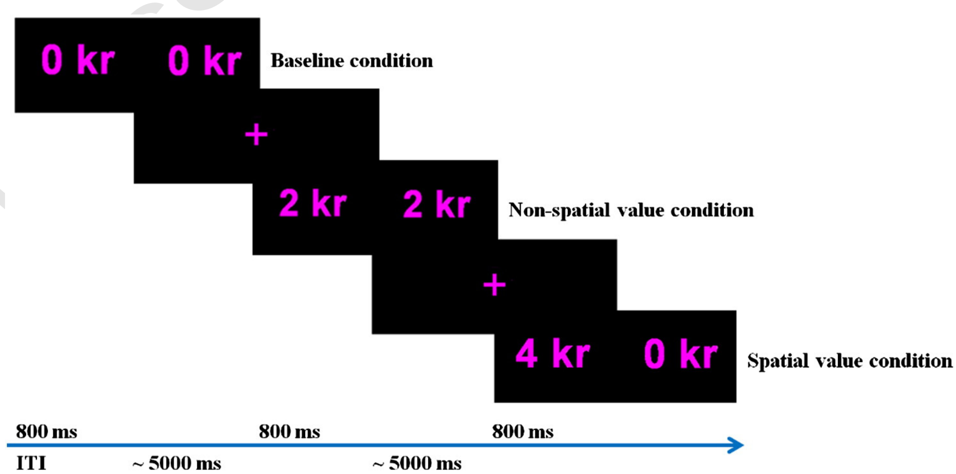

Fig. 1. The paradigm rationale. Pairs of numbers were presented horizontal to each other. The numbers corresponded to the amount the subject could win in Norwegian kroner (kr). Each pair was made up of either two similar numbers (i.e. 2–2 or 4–4) or a zero paired with a valuable stimulus (i.e. 2–0, 0–2, 4–0, 0–4). The 0–0 condition was a baseline. The task was to press the response button corresponding to the amount of kr the subject wanted to obtain.

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