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Dissociating neural variability related to stimulus quality and response times in perceptual decision-making

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ABSTRACT

According to sequential sampling models, perceptual decision-making is based on accumulation of noisy evidence towards a decision threshold. The speed with which a decision is reached is determined by both the quality of incoming sensory information and random trial-by-trial variability in the encoded stimulus representations. To investigate those decision dynamics at the neural level, participants made perceptual decisions while functional magnetic resonance imaging (fMRI) was conducted. On each trial, participants judged whether an image presented under conditions of high, medium, or low visual noise showed a piano or a chair. Higher stimulus quality (lower visual noise) was associated with increased activation in bilateral medial occipito-temporal cortex and ventral striatum. Lower stimulus quality was related to stronger activation in posterior parietal cortex (PPC) and dorsolateral prefrontal cortex (DLPFC). When stimulus quality was fixed, faster response times were associated with a positive parametric modulation of activation in medial prefrontal and orbitofrontal cortex, while slower response times were again related to more activation in PPC, DLPFC and insula. Our results suggest that distinct neural networks were sensitive to the quality of stimulus information, and to trial-to-trial variability in the encoded stimulus representations, but that reaching a decision was a consequence of their joint activity.

1. Introduction

Everyday perceptual decisions are generally made quickly and without conscious deliberation. These decisions involve comparing the sensory representations of objects encountered in the environment to memory representations of potential decision options. Making accurate perceptual decisions allows us to choose appropriate actions and behavioural responses. There has been intensive research into cognitive models underlying perceptual decisions (e.g., Bogacz et al., 2006; Brown and Heathcote, 2008; Forstmann et al., 2016; Purcell et al., 2010; Luce, 1986; Ratcliff, 1978; Smith and Ratcliff, 2004; Townsend and Ashby, 1983; Usher and McClelland, 2001; Vickers, 1979). A variety of models have been proposed that share the general idea that noisy evidence is accumulated over time until a decision threshold (criterion/boundary) is reached. Such models are known as *sequential-sampling models* (Ratcliff and Smith, 2004; Sewell and Smith, 2016; Smith and Ratcliff, 2015). These models assume that response time (RT) and accuracy depend jointly on (1) the quality of cognitive representation of the stimulus, which determines the rate at which evidence accumulates, and (2) the setting of decision threshold(s), which control how much evidence is needed before making a response. In this article, we use the diffusion decision model framework (DDM; Ratcliff, 1978; Ratcliff and McKoon, 2008) to investigate the neural correlates of perceptual decision making. The DDM has provided an account of decision-making in a variety of cognitive tasks and of the individual difference parameters that distinguish between participant populations in

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a variety of task environments (Ratcliff et al., 2015, 2016).

The DDM and other sequential-sampling models assume that trial-to-trial variability in RT and decision outcome depends on both systematic and random factors. Decision outcomes and their associated RTs depend systematically on the *quality of stimulus information,* which determines the rate at which evidence accumulates. In the DDM, the rate of evidence accumulation is termed the *drift rate*. If the quality of the stimulus information is high, then evidence will quickly and consistently accumulate towards the appropriate decision threshold. RTs are also assumed to depend systematically on the settings of decision thresholds for evidence accumulation, which are typically the same (on average) for all stimuli within an experimental block. In addition to these systematic factors, the evidence accumulation process can be perturbed by random factors, conceptualised as *noise* within the system. Noise can be external to the decision-maker (e.g., variability in the exact number of photons reaching the retina) or internal (e.g., random fluctuations in neural processing). The DDM assumes two sources of noise that affect evidence accumulation: One is trial-to-trial (or across-trial) variability; the other is moment-to-moment (or within-trial) variability. Across-trial variability reflects variability in the encoded representations of nominally equivalent stimuli. Within-trial variability represents momentary fluctuations in the neural mechanism that represents the accumulating evidence. The combined effect of these sources of noise on the evidence accumulation process is to introduce variability into the decision outcome and the RT. One presentation of a particular stimulus may lead to a fast and accurate response; another presentation of the same stimulus on a later trial may lead to a slow and/or inaccurate response.

Despite substantial progress in refining cognitive models of the decision-making process, the neural mechanisms underlying these evidence accumulation dynamics are still debated. Electrophysiology studies (for reviews see Gold and Shadlen, 2007; Romo and de Lafuente, 2013; Shadlen and Kiani, 2013) have provided evidence for a role of early sensory regions in decision-making for simple stimuli presented in different sensory modalities, including visual motion (Britten et al., 1996; Ditterich et al., 2003), tactile vibration (Romo and Salinas, 2003), and auditory stimuli of different frequencies (Tsunada et al., 2016). However, neurons in brain regions not specifically related to sensory processing have also exhibited response profiles that more directly reflect decision-making activity; e.g., the lateral intraparietal (LIP) area (Bennur and Gold, 2011; Huk et al., 2017; Roitman and Shadlen, 2002; Shadlen and Newsome, 2001), the basal ganglia (Ding and Gold, 2012, 2013) and regions involved in response preparation such as the pre-motor cortex (for button-press responses) and frontal eye fields (for saccade responses) (Gold and Shadlen, 2000; Kim and Shadlen, 1999; Selen et al., 2012; Hanks et al., 2015).

Experiments in humans using functional magnetic resonance imaging (fMRI) have also revealed an extensive network of regions involved in various stages of the decision process (for reviews see Heekeren et al., 2008; Philiastides and Heekeren, 2009; for a meta-analysis see Keuken et al., 2014). These studies also found decision-related activation in early sensory brain regions (e.g., Binder et al., 2004; Pleger et al., 2006, Serences and Boynton, 2007). Decisions about more complex visual objects have been shown to involve specialised visual regions, such as face-processing regions in inferotemporal cortex for face decisions and the lateral occipital complex (LOC) for other object decisions (e.g., Bode et al., 2012a, 2013; Heekeren et al., 2004; Tremel and Wheeler, 2015; Williams et al., 2007). It remains to be understood, however, how sensory evidence for competing choice alternatives, possibly encoded in different brain regions, is combined into one dynamically evolving unified signal that could be interpreted as a decision variable. Different regions have been suggested to fulfil such a role, including the dorsolateral prefrontal cortex (DLPFC) (Heekeren et al., 2004, 2006), the insula (Ho et al., 2009; Liu and Pleskac, 2011), and a wider network of inferior temporal, frontal and parietal regions (Hebart et al., 2012, 2016; Kayser et al., 2010a, 2010b; Ploran et al., 2007; Tosoni et al., 2008). Others have suggested that activity in some regions, including the anterior insula, anterior cingulate cortex (ACC) and DLPFC, reflects task difficulty rather than the decision process itself (Philiastides and Sajda, 2006, 2007; Philiastides et al., 2006). Several sub-cortical regions, including the basal ganglia and the subthalamic nucleus, have also been identified as part of a cortically modulated network, subserving functions such as cautiousness-moderated threshold setting, and switching from evidence accumulation to action preparation (Bogacz and Gurney, 2007; Herz et al., 2016; Forstmann et al., 2008).

Our study sought to investigate the roles of these different brain regions by disentangling two factors that were not adequately accounted for in many previous studies (with some notable exceptions; e.g., Tremel and Wheeler, 2015): *stimulus quality* and *trial-to-trial variability in the encoded representations of stimuli*, as indexed by variability in response times for fixed levels of stimulus quality. We use the term “stimulus quality” to refer to the nominal, or objective, discriminability of the stimulus, as defined by the experimenter. Trial-to-trial variability in the encoded representations encompasses the cumulative effects of noise during individual experimental trials that affect the discriminability of the presented stimulus on that particular trial. The effect of such variability can render the difficulty of the decision on any trial either easier or harder than its nominal value. We implemented a simple choice task in which participants were required to make a series of perceptual decisions between images from two object categories, pianos and chairs, that have been used successfully in previous studies (Bode et al., 2012a, 2012b, 2013), presented under different levels of discriminability (i.e., stimulus quality). Specifically, we aimed to clarify the role of object-processing visual regions as well as prefrontal and parietal brain regions, the insula and the basal ganglia. Some of these regions might be better understood as reflecting the quality of the information used to drive evidence accumulation during decision-making, while others might reflect the influence of trial-to-trial variability on the encoded representations (i.e., the effects of external and internal noise on decision information). We used a parametric regression approach for fMRI data to simultaneously search for brain regions in which activation levels were positively or negatively correlated with stimulus quality. In a second step, we searched for brain regions in which, under fixed levels of stimulus quality, activation was positively correlated with RT (slower decisions) and negatively correlated with RT (faster decisions), reflecting the influence of noise on discriminability. This approach further allowed us to investigate two aspects of “task difficulty”, namely, difficulty due to experimenter-controlled stimulus discriminability, and difficulty due to the presence of random noise on a given trial. In a last step, we correlated neural activation, which showed the respective parametric modulation with either stimulus quality or RT for fixed stimulus quality levels with various parameters of the DDM.

2. Materials and methods

2.1. Participants

Twenty-six participants took part in the study. Three data sets were not recorded due to technical problems with the acquisition hardware. The final sample consisted of 23 participants (10 female, 13 male; mean age 23.7 years, range 19–36 years). Participants were recruited via advertisements at the University of Melbourne and Monash University. They had no history of neurological disorders, no contra-indicators for fMRI, were right-handed, and had normal or corrected-to-normal visual acuity. All participants gave written informed consent before participation, and they were compensated for their time with AUD 40. The study was approved by the human research ethics committee of Monash University (CF12/1399–2012000734), Australia, and conducted in accordance with the Declaration of Helsinki.