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Representational precision in visual cortex reveals outcome encoding and reward modulation during action preparation

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ABSTRACT

According to ideomotor theory, goal-directed action involves the active perceptual anticipation of actions and their associated effects. We used multivariate analysis of fMRI data to test if preparation of an action promotes precision in the perceptual representation of the action. In addition, we tested how reward magnitude modulates this effect. Finally, we examined how expectation and uncertainty impact neural precision in the motor cortex. In line with our predictions, preparation of a hand or face action increased the precision of neural activation patterns in the extrastriate body area (EBA) and fusiform face area (FFA), respectively. The size of this effect of anticipation predicted individuals' efficiency at performing the prepared action. In addition, increasing reward magnitude increased the precision of perceptual representations in both EBA and FFA although this effect was limited to the group of participants that learned to associate face actions with high reward. Surprisingly, examination of representations in the hand motor cortex and face motor cortex yielded effects in the opposite direction. Our findings demonstrate that the precision of representations in visual and motor areas provides an important neural signature of the sensorimotor representations involved in goal-directed action.

Introduction

Sensorimotor interactions with the environment provide organisms with information about the consequences of their actions. Such information is critical for developing outcome-directed, goal-driven behavior. According to ideomotor theory (Harleß, 1861; James, 1890; Lotze, 1852), goal-directed action involves the anticipation of the action's perceptual consequences. This prediction has been confirmed in numerous behavioral studies (Elsner and Hommel, 2001; Shin et al., 2010; Waszak et al., 2012). There is also a growing literature beginning to reveal how perceptual and affective features of intended outcomes are processed in the brain (Daw and O'Doherty, 2014; Elsner et al., 2002; Jessup and O'Doherty, 2014; Kühn et al., 2011, 2010; McNamee et al., 2013; Melcher et al., 2008; Valentin et al., 2007). The present

study focused on the nature of the perceptual representations in visual cortex. Kühn et al. (2011) have shown that category-specific perceptual regions code the outcome of intended actions, whereby the preparation of hand versus face actions activates category-specific areas that have traditionally been associated with the perception of face stimuli (FFA) and body parts (including hands; EBA) (Downing et al., 2001), respectively.

Here we address the question whether perceptual representations of anticipated action outcomes in EBA and FFA show an additional signature of enhanced neural encoding. We used multivariate analysis of fMRI data to examine the consistency, or precision, of patterns of activity in the EBA and FFA across trials. Our choice of analysis is motivated by previous research demonstrating that representational precision has important functional implications in neural processing

(Churchland et al., 2011, 2010, 2006; Schurger et al., 2015, 2010; Warren et al., 2016, 2015). Furthermore, the multivariate measure of precision we use does not depend on a uniform increase of brain activity in all voxels of a given brain area. Thus, as earlier work using multivariate techniques has shown, it allows us to characterize changes in neural processing even in cases when the change is not detectable using univariate approaches (Etzel et al., 2016; Xue et al., 2010).

Neurophysiological studies in animals have shown that measures of representational precision are a signature of information encoding in many parts of the cortex (Churchland et al., 2011, 2010, 2006). M.M. Churchland and colleagues demonstrated that the variability of firing rates of neurons in the premotor cortex decreases as a decision is formed Churchland et al. (2006), and this type of variability decreases across the whole brain at onset of any type of stimulus (2010). In humans, Schurger and colleagues demonstrated that neural consistency is a hallmark of conscious perception, both between (2010) and within (2015) trials. Here we attempt to demonstrate for the first time that modulations in representational consistency can also be region specific. More specifically, we examined representational consistency to determine whether anticipation of a hand or face action increases the precision of representations in the associated perceptual area, i.e. the EBA or FFA (see Fig. 1).

The second goal of the present study was to test whether the neural consistency of sensorimotor codes during action preparation is modulated by the reward value of a particular outcome (see Fig. 1C, middle and right panel). Recent work suggests that reward motivation impacts the signal-to-noise ratio of representations of task sets in frontoparietal brain regions (Etzel et al., 2016). This finding is consistent with long-standing theoretical accounts (Botvinick and Braver, 2015; Kruglanski et al., 2002; Simon, 1967). Based on recent behavioral evidence, we predict that neural representations of perceptual outcomes should be more precise specifically when the related actions are associated with reward (Allman et al., 2010; Eder and Dignath, 2015; Muhle-Karbe and Krebs, 2012) (Fig. 1C middle panel). Alternatively, potential reward might have a more general neuromodulatory effect related to motivational significance, whereby increases in catecholinergic-mediated gain improve the signal-to-noise ratio of neural processing across the brain (Aston-Jones and Cohen, 2005; Nieuwenhuis et al., 2005; Servan-Schreiber et al., 1990). Such an effect may provide a general boost in stability or precision (Warren et al., 2016, 2015) (Fig. 1C right panel). Interestingly, Warren, Holroyd, (2011, 2012) argued that brain-wide increases in signal-to-noise ratio should have a differential impact across brain regions, such that brain regions more engaged in signal processing should have a greater change in activity than less engaged regions. Thus, region-specific effects of reward on neural precision do not necessarily discount a role of neuromodulators in this effect.

Finally, we also investigated the precision of motor representations of planned actions. In our task, participants were cued as to whether they would be required to make either a hand or face action three to six seconds later. Critically, during this cue period, participants did not know exactly which hand action (left or right button press) or face action ("smile" or "kiss") they would make, only whether they would use their hands or their face. We expected that representations of potential actions would be strongly instantiated in motor cortex relative to the same action representations when they were not anticipated. However, the impact that such a change should have on representational precision is not clear. One possibility is that strong representation of both actions simultaneously should promote consistency between trials. Another possibility is that the uncertainty concerning which action would ultimately be cued would provoke greater variability, reducing precision. Notably, A.K. Churchland et al. (2011) showed that firing rates of neurons in the primate lateral intraparietal area are more variable when monkeys are cued with four versus two potential decision outcomes. Furthermore, within trials, firing rates in this area get more variable as a perceptual decision is

formed. They hold that neural variability is a natural outcome of the stochastic accumulation and integration of evidence (Miller and Wang, 2006). Though our participants do not make protracted decisions based on noisy evidence, they do consider multiple decision outcomes. Also potentially relevant is that information encoded in perceptual areas versus motor areas involves different levels of abstraction (Wurm and Lingnau, 2015). For example, representations in the FFA and surrounding regions are distributed and overlapping (Haxby et al., 2001). In contrast, representation of left versus right hand responses will be lateralized and, consequently, discrete. Warren et al. (2016) demonstrated that the effect of neural gain on representational precision varies according to pattern overlap. Thus, if action relevance were to increase representational precision through modulation of gain either locally (Destexhe et al., 2003), or across the brain (Warren et al., 2016), we would expect precision to increase more in perceptual regions than motor regions. However, a change in precision in motor cortex opposite to that observed in perceptual areas would work against an interpretation of these effects as being mediated by brain-wide changes in signal-to-noise ratio.

To foreshadow our somewhat counterintuitive results, we found that whereas considering motor actions increased representational precision in perceptual areas associated with the action (EBA versus FFA), it decreased representational precision in associated motor areas (hand motor cortex versus face motor cortex). Furthermore, with some caveats, we found evidence that increasing reward magnitude increases representational precision in perceptual areas, but decreases representational precision in motor areas, apparently enhancing the effect of action-area congruence.

Material and methods

Participants

Thirty-one healthy right-handed volunteers (age 19–27 years; 8 males) with normal vision and no dental braces participated in the study. The experiment was approved by the medical ethics committee of the Leiden University Medical Center, and all participants gave written informed consent. The experiment took approximately two hours, and participants were paid 25 euros. One participant was excluded from analyses because of a hardware failure during data collection. Participants were randomly assigned to one of the two action-reward mapping groups: Half of the participants (n=15) learned to associate face actions with high reward and hand actions with low reward. The other half of the participant (n=15) learned to associate hand actions with high reward and face actions with low reward.

Experimental paradigm and design

Fig. 1B shows the trial structure of the task. Each trial started with a cue presented for 1 s showing the picture of a house. There were two possible house pictures, each cuing a different condition. The house cues instructed participants to either respond with a face or hand action as soon as the subsequent target was presented (see Fig. 1A). Note that the brain response to this action-preparation phase is the focus of the analyses described in this paper. After a blank screen of jittered duration between 2 and 5 s, the target specifying the to-be-performed action was presented for 1 s. The three possible actions in the context of a hand cue were a button press with the left index finger, a button press with the right index finger, or no action. The three possible actions in the context of a face cue were uncompressing the lips into a broad smile and raising both eyebrows ("smile"), compressing the lips into a kiss and lowering the eyebrows ("kiss"), or no action (Fig. 1A). Participants were instructed to respond quickly, but due to the difficulty of measuring the timing of face actions, we followed Kühn et al. (2011), and measured reaction times for the hand actions only. Following target presentation, there was a two-second blank screen,