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Action selection: A race model for selected and non-selected actions distinguishes the contribution of premotor and prefrontal areas

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ABSTRACT

Race models have been used to explain perceptual, motor and oculomotor decisions. Here we developed a race model to explain how human subjects select actions when there are no overt rewards and no external cues to specify which action to make. Critically, we were able to estimate the cumulative activity of neuronal decision-units for selected *and* non-selected actions. We used functional magnetic resonance imaging (fMRI) to test for regional brain activity that correlated with the predictions of this race model. Activity in the pre-SMA, cingulate motor and premotor areas correlated with prospective selection between responses according to the race model. Activity in the lateral prefrontal cortex did not correlate with the race model, even though this area was active during action selection. This activity related to the degree to which individuals switched between alternative actions. Crucially, a follow-up experiment showed that it was not present on the first trial. Taken together, these results suggest that the lateral prefrontal cortex is not the source for the generation of action. It is more likely that it is involved in switching to alternatives or monitoring previous actions. Thus, our experiment shows the power of the race model in distinguishing the contribution of different areas in the selection of action.

Race models can account for many behavioural, perceptual and oculomotor decisions (Carpenter and McDonald, 2006; Gold and Shadlen, 2007; Ratcliff and Rouder, 1998) based on trial to trial variations in a race between alternative responses. In race models, and related drift diffusion models, activity of neuronal decision-units rises from baseline to a threshold that represents commitment to a response (Churchland et al., 2008; Roitman and Shadlen, 2002; Yang and Shadlen, 2007). Here we apply a race model to action selection when there were no overt rewards and no external stimulus to specify 'correct' actions. There are two lines of neurophysiological evidence to suggest that race models are relevant to decisions of this sort. Firstly, if monkeys are taught to base their decision on the direction of coherently moving dots, accumulating neuronal activity is found that reflects the decision even when there is no coherent motion and both choices are equally rewarded (Churchland et al., 2008; Roitman and Shadlen, 2002.). Secondly, the decision threshold for a selected action is constant, whether or not it is specifically cued.

Here we developed a race model and used fMRI to identify brain activations that reflect parameters of this model (see Fig. 1 and Methods). In our model, action selection emerges from the race between competitive decision-units, each associated with distinct action schemas for permitted responses (Norman and Shallice, 1980). Motor decision-unit activity rises from baseline to response threshold with a Gaussian rate distribution. Based on the parameters of these decision units, we estimated accumulated metabolic activity (EAA) for each trial. The trial-by-trial estimates of EAA informed the analysis of fMRI data. Critically, we were able to estimate the total demands of both the 'winner' and 'losers' of the race, using the Inverse Mills Ratio for truncated Gaussian distributions (losers are truncated by the 'winner' reaching the response threshold).

We chose a task that has frequently been used in the human imaging literature, with reproducible data on the brain regions that are involved. Human participants chose between manual responses where there were no overt rewards and there was no external stimulus to guide one action rather than another. This is associated with reproducible differential activation of dorsal prefrontal cortex, the pre-SMA and the intra-parietal cortex (Deiber et al., 1991; Forstmann et al., 2008; Frith et al., 1991; Rowe et al., 2005, 2008). However, the different roles of these regions are less well understood and activations may arise because of different cognitive operations even within such an apparently simple task (Lau et al, 2004).

Therefore, our fMRI analysis also included a categorical term that distinguished specified from selected responses, in addition to the EAA that is related to trial to trial variation in response decisions. This approach allows us to distinguish the selection between action schemas from other processes which, although temporally associated

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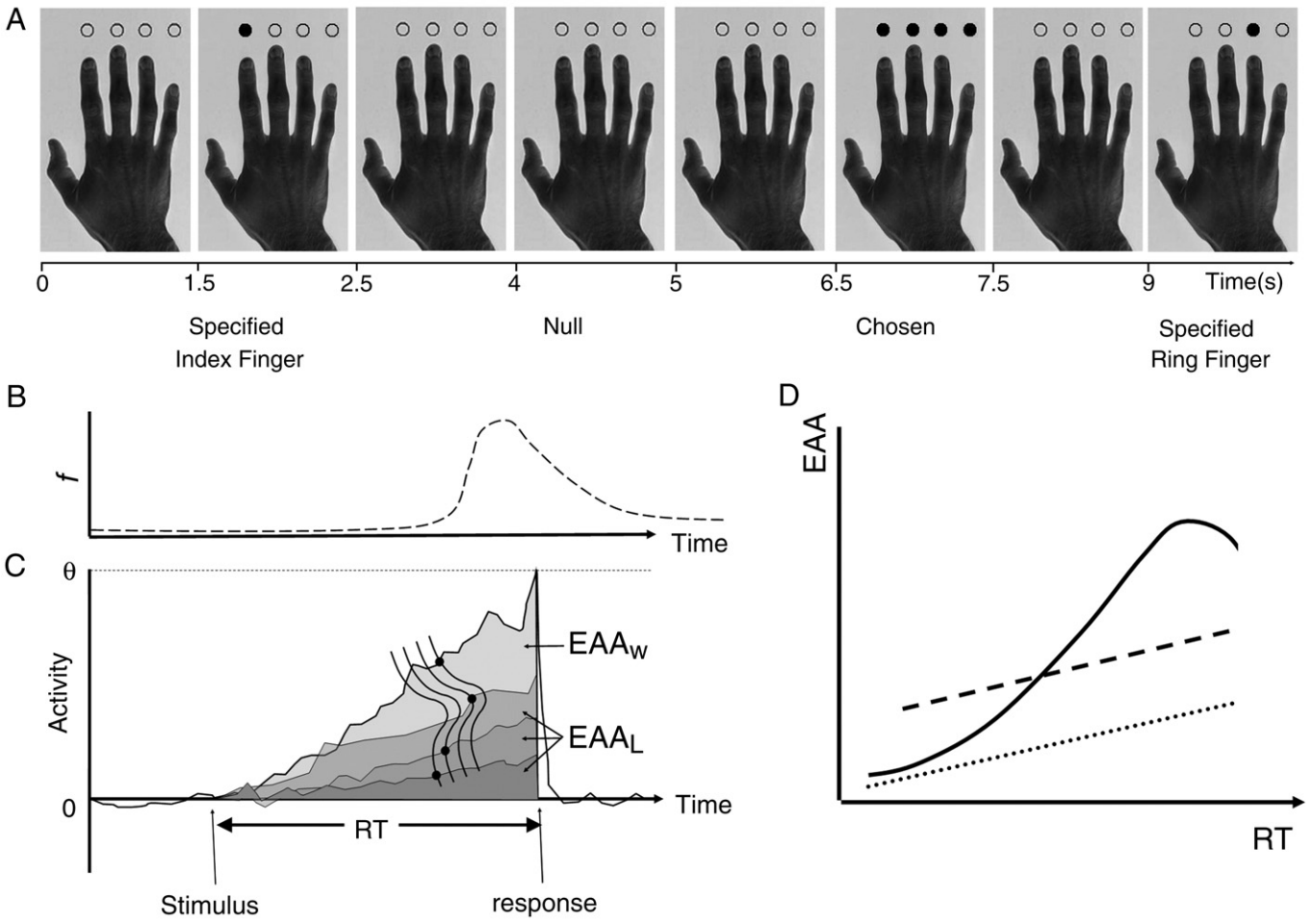

Fig. 1. (A) The task required subjects to perform a specified button press (Specified condition) as indicated by a single dot above the corresponding finger of a picture of a hand, or to choose one of the four possible button responses (Chosen condition). (B, C) schematic representations of the skewed distribution of reaction times (RT), arising from the Gaussian distribution of speed of response. A response results from a decision processor drifting between baseline activity 0 and a threshold θ. The estimated accumulated activity (EAA, grey shading) above baseline in the race model is a function of the threshold and RT and can be estimated for winners (EAA_W) and losers (EAA_L) in the race (see Methods). With four decision units drifting to threshold with a common underlying Gaussian distribution, the winner is the one at the faster (left) hand end of the rate distribution (upper black dot) whereas the other three losing decision units on this trial are at slower points on the rate distribution (lower three black dots). (D) Schematic representation of total EAA in relation to RT. The EAA for specified responses is linearly associated with the RT in the race model (dotted line). For chosen responses, the EAA is a non-linear function of RT (solid line), approximating the value for specified trials at very short and very long RTs, but greater than specified trials for intermediate RTs. The precise shape of this non-linear relationship depends on the subject-specific values of mean 1/RT and its variance. The effect of a categorical difference between trial types, due to an additional non-race 'choice' process, is illustrated by dashed lines.

with selection, are not the mechanism of selection itself e.g. memory or monitoring of recent responses to modulate future response selection. Because these occur over a series of trials, we also performed a second study in which we measured activity for action selection on the first trial alone. Activity on this trial must reflect selection rather than memory.

The present study had three aims. The first aim was to test the application of the race model to the selection of human manual responses when multiple responses are permitted. The second aim was to see whether it can distinguish between the contributions of different cortical areas to response selection. The final aim was to understand how selection on one trial is influenced by the context of recent actions.

Methods

Subjects and task

For the first study, twenty healthy adults participated (age range 19–40, mean 26 years, 10 men). For the second study, fifty seven subjects participated (range 18–75, mean 43 years, 31 males). None had a history of significant neurological or psychiatric illness. The studies were given a favourable opinion by the local Research Ethics Committee and participants gave written informed consent.

The task is at first glance simple: subjects made button presses with one of four fingers of the right hand. In the main study, for a third of trials, a response was 'specified' in time and position by a filled in dot above the picture of a hand for 1 s (Specified condition). On another third of trials, the subjects chose which finger to press, in response to a similar visual cue in which all circles were filled in for 1 s (Chosen condition). See Fig. 1 for example cues. A third of trials were 'null' trials which included continuous presentation of the hand picture with no change in colour of the dots. The trial order was randomised, and stimulus onset asynchrony was 2.5 s. For the subsidiary study, the stimuli were similar, and the first response was either chosen or specified as above. Subsequent trials however differed for some subjects in terms of the trial order, being either blocked or randomised.

Despite the apparent simplicity of the task, we were specific in the supplementary instructions during training and immediately prior to scanning. For the Chosen condition, subjects were asked to "make a fresh choice on each trial using any of the four buttons, regardless of what you have done before". We did not ask participants to make a