Title Neural Mechanisms of Hierarchical Planning during Navigation

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Humans and other animals often have to plan behaviour over multiple steps in order to receive a positive outcome. Understanding how they do this is a challenge for psychologists and neuroscientists, because the number of possible future states grows exponentially with time as an agent looks ahead. One suggestion is that humans represent decision environments hierarchically, planning over a series of interim goals (subgoal) in order to reach a final goal. However, evidence for this view remains scarce, and little is known about the potential neural underpinnings of hierarchical planning. In this study, we aim to find evidence for the existence of subgoals in a navigation task with humans, and to identify the brain regions involved during the execution of a plan.

We used fMRI to measure BOLD signal while 20 healthy participants (10 female; age 19-34, mean 25.6 years) performed a navigation task within a previously-learned virtual environment representing a subway network. Stations were connected via "subway lines" that (during training) were represented with a salient contextual cue (colour). We reasoned that stations where the lines intersected (exchange stations) would be treated as subgoals and predicted that they would garner unique behavioural and neural effects, even though during task performance they were not associated with explicit visual cues.

Participants first performed a training session, during which they became familiar with the subway map by repeatedly completing journeys to a destination station. They executed their plan by pressing a key to move in one of the cardinal directions (north, south, west, east) at each station, and an additional action (switch) to change between lines at an exchange station. Finally, once they reached the destination station, participants received feedback on the duration of their journey (and the optimal distance). During training only, participants could see a map of the network, and were quizzed about it to ensure that they were learning.

On a subsequent day, participants undertook a second session whilst undergoing whole-brain fMRI. In the scanner they also completed multiple journeys but the colour of the lines were removed and no additional action was required to switch between lines. Participants earned bonus income by reaching their goal on time, and thus tried to minimise the absolute distance of their paths. Journeys were randomly cancelled with fixed probability on each time step, to put pressure on participants to decorrelate key experimental variables for imaging anlaysis.

Reaction times increased as the subject approached a line change, and then speeded up directly after the change. Critically, this did not happen around exchange stations where the subject did not change lines. A similar but weaker effect was found near elbow stations, where the subject changed direction but not line.

On the neural level, we observed higher activation in the bilateral dorsolateral prefrontal cortex when an exchange station was reached, which was independent of a line change, suggestive of processing the demand associated with changing context (or not). An increase of activation in the motor and premotor cortices was observed for a switch of direction (i.e. response) from the previous trial, independently of being in an exchange station or not. Specifically for line-changes, i.e. when the response was changed *and* it was an exchange station, we found higher activation in a network of right caudate nucleus, thalamus, and the supplementary motor area. In other words, these regions may signal the need to switch to a new context at a subgoal state. Meanwhile, activity in ventromedial prefrontal cortex (vmPFC) increased as subjects approached the final destination, as if it were encoding proximity to a goal state.

These results provide evidence that humans make use of hierarchical representations in order to plan their route during navigation, and that the striatum and interconnected structures signal when an interim goal has been reached. Simultaneoulsy, the prefontal cortex deals with higher-level functions, with lateral regions processing the cognitive demand, and more medial regions monitoring performance in the task.