The influence of recent decisions on future goal selection

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Recent decisions about actions and goals can have effects on future choices. Several studies have shown an effect of the previous trial history on neural activity in a subsequent trial. Often, but not always, these effects originate from task requirements that make it necessary to maintain access to previous trial information to make future decisions. Maintaining the information about recent decisions and their outcomes can play an important role in both adapting to new contingencies and learning. Previous goal decisions must be distinguished from goals that are currently being planned to avoid perseveration or more general errors. Output monitoring is probably based on this separation of accomplished past goals from pending future goals that are being pursued. Behaviourally, it has been shown that the history context can influence the location, error rate and latency of successive responses. We will review the neurophysiological studies in the literature, including data from our laboratory, which support a role for the frontal lobe in tracking previous goal selections and outputs when new goals need to be accomplished.

1. Introduction

Every action that we perform is influenced by past experiences, at least to some extent. However, for many years, behavioural neurophysiologists have studied the neural correlates of behaviour in non-human primates by only examining the events taking place within a trial. Within each trial, experimenters, including us [1–4], have compared neural activities in a number of conditions, such as the activity associated with movements towards spatial targets or the responses to different stimuli, either in a blocked- or mixed-trial design. In each trial, a given condition was considered to be equivalent to all others for that same condition. Thus, both tasks with elevated cognitive loads and learning tasks [5–7] were studied using this approach.

Only recently, when the new task designs began to explicitly require the use of past information, have several laboratories extended their analyses to time scales longer than a single trial. Specifically, they developed new analytical tools that could classify a trial based on its previous and future history [8] and could track the time course of processes or events evolving in time over multiple trials. Several recent studies have analysed the relationship between neural activity and trial history for learning [9], strategy application [10,11], outcomes [10,12], and motor control and adaptation [13].

Herein, we will examine the effects of trial history on neural activity in certain areas of the frontal lobe that are primarily part of the dorsal stream [14]. We mainly focus on the results of our previous experiments using the countermanding task in the dorsal premotor cortex (PMd) and strategy and magnitude discrimination tasks in the dorsal prefrontal cortex (PFd). The prefrontal (PF) and premotor (PM) cortex areas occupy different positions in the cortex organization in terms of processing hierarchy [15]. As a consequence of anatomical and functional differences, different paradigms have been used to study the effects of trial history on neural activity in these areas. For motor-related areas, such as the PM cortex, the paradigms adopted were often ideal for exploring the history effect on the control of motor output. For areas in the PF cortex, the paradigms designed were more suited to study abstract goal generation and strategy implementation [11,16].
2. Recent actions impact future behaviour and neural activity

To optimize performance, behaviour can be influenced by both immediate and recent circumstances to allow for continuous adaptation to contextual environmental changes. Contributing to the proper anticipation of task requirements, this type of monitoring of past actions is often referred to as a proactive control. Following contextual demands, the overall effect is either positive or negative according to existing rules, information, conflicts, expectancies or competing motor solutions that characterize how subjects are instructed or trained [13]. For example, the reaction time (RT) to a target presented among distractors decreases after repeated presentation; however, when one of the previously identified distractors is abruptly indicated to be a target, repeated presentation corresponds to reduced performance, as in the negative priming effect [16]. Mostly explored in human and non-human primates, previous trial effects have been described for different task sets by measuring behaviourally the different levels of cost versus benefit and conflict [17].

Neurophysiological support for trial history effects has been explored using different motor tasks, in particular within the oculomotor domain; all available results suggest that the effects depend on the influence of the previous trial on the efficiency and functions of different neural mechanisms [13]. A good example is the antisaccade task (figure 1a). Subjects are instructed in different trials by a visual cue if the required eye movement is directed towards either the target or an opposite location. Good performance for generating an antisaccade response requires the suppression of the reflexive movement and a new saccade generation. Behavioural evidence shows that after executing an antisaccade trial, the inhibitory modulation remains sustained and, therefore, the saccade (and sometimes the antisaccade) preparation is usually delayed [18]. Indeed, such subjects display longer RTs and worse performance. In humans, procrastination following antisaccade has been associated with neural modulation in the frontal eye field (FEF) and PF measured using magnetoencephalography [19] and functional magnetic resonance imaging [20] approaches.

Observational findings in humans agree with neurophysiological studies in monkeys that have associated longer latencies of motor execution with lower preparatory activity in the FEF [21,22]. It is likely that neurons in the FEF reduce motor-related activity, allowing for adaptive monitoring that includes suppression under the modulatory control of other PF areas [23].

Recently, the countermanding task has been used to study the neural correlates of trial history effects (figure 1b; [24,25]), exploiting inhibitory control both in the oculomotor domain [26] and during reaching arm movement generation [27–29]. The task includes both trials where a motor response is required (go trials) following the presentation of the target, and a smaller number of trials (stop trials), for which the interruption of the programmed movement is required because an imperative stop signal is presented during the RT. The task is different from the antisaccade task and from other tasks that explore motor inhibition, as the information is provided only after a motor plan is developed. Neural activities have been explored in different oculomotor and some skeletonotor areas of the brain, such as the FEF, superior collicolus, PMd, supplementary motor area (SMA) and pre-SMA (figure 2a).

In the classical theoretical construct (race model; figure 2b [24]), behavioural performance in the stop trials is the result of competitive interactions between the two processes. The go process is activated by target presentation, favouring the motor response, whereas the stop process is activated by stop signal presentation, resulting in motor plan cancellation; erroneous movements or successful cancellations are the result of a threshold-based mechanism. Using the race model, the probability of cancelled stop trials obtained by varying the time of presentation of the stop signal after the go signal is presented (stop signal delay, SSD) and the go process duration (average RT) are used to estimate the speed of the stop process. These parameters yield a measure of the reactive response to stop signal presentation, which is also referred to as the stop signal reaction time (SSRT). A well-described effect of proactive control in this task is the elongation of the RT in go trials following trials with stop signal presentation [30], which corresponds to an increased probability of success in case of a further stop trial appearance [28,31]. The observation that a recent trial sequence can influence performance in the countermanding task suggests that factors other than the outcome of the two competitive processes in the race might play a role [27,29,30,32–36].

**Figure 1.** An oculomotor-based model of the antisaccade and countermanding tasks. (a) In the antisaccade task, a visually presented cue (green, upper panel; red, bottom panel) instructs for the type of movement required (prosaccade (green) or antisaccade (red)). (b) In the countermanding task, motor inhibition is a consequence of stop signal presentation (red, central stimulus) during the reaction time (RT). SSD, stop signal delay.
Furthermore, what emerges is that the countermanding task is ideal for studying correlates of both reactive and proactive control in the same neural population. Accordingly, in a recent study by Pouget et al. [26] that used an oculomotor version of the countermanding tasks and recorded single unit activity, the authors showed that response procrastination after the stop appearance was accomplished by modulation of the starting time of the preparatory activity accumulation in the FEF and SC, two important centres in the cortico–subcortical network that control eye movement generation [37]. Both areas have been previously shown to be important in reactive control; in stop trials, FEF and SC neurons modulate their activity before the end of the behavioural estimate of stop process ending time (i.e. the SSRT [38,39]) (figure 2c,d).

In the skeletomotor system, two areas have recently been explored in the PM cortex. In the SMA, a mesial PM area influencing the spinal cord and other cortical motor centres in the frontal lobe but unable to participate directly in the control of motor generation [40], single unit activity, multunit activity or local field potentials (LFPs)—activities, with slight differences, are related to the level of proactive control [27]. Surprisingly, in the PMd, where neurons predict whether an action will be executed in stop trials (these neurons have similar characteristics as FEF neurons; see Discussion in [41]), a different relationship of history-dependent behavioural performance and neural modulation was reported by Marcos et al. [28]. These authors showed that the PMd informs response adjustments following different types of trials only by across-trial firing variability, measured as variance of the conditional expectation [42], and not by changes in the average single unit firing rate (figure 2c,d).

Human studies using the countermanding task have suggested an important role for either the PE, mostly at the level of the ventrolateral portion, in both reactive and proactive control, or the SMA [43,44], with pending controversies.
Unfortunately, the role of the PM regions has not yet been fully explored in humans (but see [45]).

In conclusion, converging evidence suggests that proactive control and trial history modulate frontal lobe areas that often overlap. However, for the effects observed in the countermanding task, differences are apparent between the oculomotor and skeletonmotor systems. For example, while we know a great deal about many oculomotor-related centres, the same is not true for arm/hand movement control. Indeed, the primary motor cortex has not yet been explored in animal models using effective paradigms.

Moreover, different signals (LFP, single unit or across-trial neural variability) seem to be important in different nodes of the frontal lobe network. The effect on neural variability and the lack of effects on the PMd discharge rate suggest that different populations can mutually suppress each other and could be involved in actions monitored under the influence of remote inputs [28,46]. However, characterizing both the relationship between the different types of signals during adaptive behaviour control and the roles of other yet to be explored areas of the brain will require further exploration.

3. Previous goal encoding in the prefrontal cortex

In this section, we will examine the importance of previous trial choices on the modulation of neural activity in the context of goal encoding, focusing mainly on the PFD cortex. Cells that encode goals have been identified in recent studies throughout many brain areas. In this review, we define a goal as the object or location that an animal chooses as the target for its actions.

Several studies have emphasized the role of the PFD or ventral PF (PFv) [11,15,47–49], in addition to the PM and basal ganglia [50–52] in goal encoding. Based on their position in the goal encoding hierarchy, the PFD and PM areas play different roles in goal encoding. The PFD and PM cortex, as emphasized by Passingham & Wise [15], occupy different positions in the context of this hierarchy that depend on their anatomical connectivity. The PFD, but not the PM, receives visual and auditory inputs and the conjunction of stimulus-outcome representations from the orbital PF cortex, and the PM is closer to motor specification because of its direct projections to the motor cortex and spinal cord.

Moreover, in the PFD, but not the PM cortex, different outcomes can be evaluated at the level of the orbital PF cortex [53], offering the degree of signal combination necessary to integrate outcomes and choices that the PM cortex lacks.

From an evolutionary perspective, Genovesio et al. [54] have recently proposed that PFD–PPC (posterior parietal cortex) networks evolved in anthropoids to allow rapid learning, for which foraging goals were chosen based on relative metrics. PFD and PPC neurons share a representation of relative metrics such as ‘greater than’ in the temporal, numeric and spatial domains [55,49]. Within this network, goal encoding by the PFD is characterized by the following: (i) the conjunctive nature of goal representation with other information, such as distance, numbers, order and duration [49,56,57] and (ii) the independence of goal representation from the means to reach those goals [48–50].

Recently, an increasing number of studies have started to explore the role of the PFD in representing the history of goals [10,11] and outcomes [10,58], whereas previous studies examined the persistence of neural activity both in terms of working memory for sensory stimuli and of delayed memory signals for future goals [50,59,60]. Although previous goals and outcomes are not only represented in PFD, but are also more widely represented in the anterior cingulate cortex, lateral intraparietal area and supplementary eye field (SEF [61]), here we will focus mainly on the PFD cortex and discuss the results from some neurophysiological studies in monkeys that addressed this topic by adopting two tasks, strategy and distance discrimination.

By adopting a strategy task (figure 3a,b), Genovesio et al. [7,11] explored the representation of previous goal information. In this task, the monkeys needed to choose a spatial goal based, but not solely, on the most recent goal [7]. If the cue at the beginning of the trial was repeated, the monkeys needed to stay with the same spatial goal (left, right or up) as in the previous trial; if the cue changed, the monkeys needed to shift to a different spatial goal. To perform the task, the monkeys had to maintain in memory first the previous goal location between trials (figure 3b), and later the future goal information in the delay period preceding the response. Genovesio et al. [11] found that previous and future spatial goal information are encoded by separate populations of neurons (figure 3c), with few exceptions (hybrid cells), although they overlap in the same area. In figure 3d, the time course of previous and future goal signals are shown separately for the two populations of cells. When the previous goal representation declined during the trial, future goal encoding increased in strength soon after a decision could be made regarding the next goal. The separation between previous and future goal-selective cells contrasts with the high proportion of PF neurons with conjunctive representations of goals and strategy signals; 46% of the strategy cells were modulated by the conjunction of strategy and future goals [7].

As another example of conjunctive encoding, Warden & Miller [62] described PF neurons representing multiple objects in a combined manner that are presented sequentially in a working memory task. We have hypothesized [11,63] that this separation between networks encoding past and future might support output-monitoring functions. Output monitoring refers to monitoring of the goals that have been accomplished and those that remain pending. Its failure can determine omissions when an intended pending goal is represented as already accomplished, such as in habitual or repetitive tasks, and a higher level of monitoring errors are found in schizophrenia and Alzheimer patients [64–67].

Tsujimoto et al. [68] examined the correlation between neuron pairs recorded simultaneously in a strategy task. They analysed the correlation between different pairs of neurons, with neuron pairs encoding previous goals (P–P pair), future goals (F–F pair) or both a previous and a future goal (F–P pair). They found that future goal, but not previous goal maintenance was associated with correlated activity between neuron pairs (figure 3e). Additionally, F–P neuron pairs showed correlated activity, although the prevalence of negative correlations contrasted with the positive correlations that characterized the F–F pairs. The F–P pair correlations could represent a means to bridge past and future choices but could also subvert a more general monitoring function. The presence of a correlated activity between F–F, but not P–P neuronal pairs, could indicate that correlated activity is
required for transforming a future goal signal into an action by temporal and spatial summation mechanisms, through a projection on the same target neurons that specify an action.

In another experiment, Tsujimoto et al. [69–71] studied the representation of the previous spatial goal in a cue strategy task in which different cues instructed either a stay or a shift strategy. They found, in line with the results described above [7], that the PFd encoded the previous goal, which was in contrast to the absence of previous goal signals in both the orbitofrontal cortex and the frontal pole cortex, pointing to PFd specificity within the PF cortex in previous trial goal encoding. This result indicates that previous goal signals are not ubiquitously represented in the frontal cortex.

Previous goals and outcomes can also be maintained in memory apart from output monitoring functions, also to update the value functions of different alternatives (see [72] for a review). Indeed, reinforcement learning models have taken into account the previous history of reward and states [73]. It has also been shown that during learning, the previous outcome can enhance the neural representation of the
future saccade direction in a stimulus–response association task in both the PFd and caudate nucleus [9], suggesting that previous trial signals can have a variety of functions.

4. Does previous goal encoding depend on task relevance?

Several studies have assigned a general monitoring function to the PFd. The task that traditionally has been used to assess the monitoring role of the PFd is the self-ordered task. This task requires monitoring previously selected objects, because once an object has been selected, the object should be discarded through an elimination process. In support of the monitoring function of the PFd, lesions in the PFd cause impairment in this task in monkeys [74] and imaging studies in humans have shown PFd activation during self-ordered tasks [75].

Recently, we asked whether goal monitoring occurs automatically—indicating instances when it is not important for task performance [76]. Several studies have previously shown that information can be encoded in the PFd, even when it is irrelevant (at least under some conditions) [77,78], suggesting that similarly past goals might even be encoded when they are irrelevant. PFd cells represent the previous goal information not only when the monkeys were required to remember the previous location in the strategy task, but also in a spatial delayed-response task [71] that did not require holding any previous trial information in memory. Although this signal could represent a case of encoding an irrelevant previous goal, it remains possible that it emerged only as a consequence of the training history of the monkey in the strategy task that required monitoring.

More recently, we studied [76] previous goal representation in the PFd and periarcuate cortex (PA) in a distance discrimination task (figure 4a), in which the task of the monkey did not require previous trial monitoring and the monkeys were not trained in other tasks that required it. In this task, the monkeys were instructed to determine which of two stimuli, presented sequentially at different distances from the screen centre, was the farthest away. The task did not require any monitoring of the previous trial, because the trials were independent from each other. We found that the representation of the previous goal and outcome were maintained in the current trial, although it did not have relevance for task performance. PFd neurons encoded the previous goal, both in terms of its location and features, in addition to the previous outcome (correct or erroneous). Figure 4b shows that PFd neurons encoded both the location and features of the previous choice, and a conjunctive representation of previous goals and outcomes (figure 4b, Venn diagram).

More notably, in contrast to this positive result, PFd cells did not maintain other information associated with the second stimulus presented in the previous trial, such as its location (above and below the screen centre), distance or features (red or blue), some of which were relevant in the context of the previous trial. Future studies should examine whether monitoring of non-goal information might emerge when animals are faced with sudden task rule changes and, if so, whether it would limit the generalizability of these results showing a selective encoding of past goal information only in stable environments.

The presence of the goal signals described above is instructive, especially when compared with the lack of stimulus colour and shape information from the previous trial in the strategy task [11]. In fact, in the strategy task, the information about the identity of the previous stimulus was not
only relevant, it also was essential for the task performance in the strategy task. Nevertheless, we did not find cells that encoded non-spatial features of the previous non-goal stimulus, although we did find neurons that responded to visual stimulus presentation in the current trial. Thus we could not identify any previous stimulus encoding, although the previous stimulus was relevant for task performance in the strategy task [11]. However, we did observe past object goal encoding in the distance discrimination task, even when it was not relevant [76]. This difference could depend on the fact that the previous encoded object in the distance task had also been a goal in the previous trial, whereas in the strategy task the highly relevant previous object did not serve as a goal.

More notably, our task design [76] allowed us to compare the relative strength of irrelevant spatial goal information with that of relevant spatial information that was not a goal within the same distance discrimination experiment [56]. We found that only 9% of cells encoded the distance of the first stimulus presented from the reference point during the delay period, although its evaluation was necessary for the task performance. Notwithstanding its relevance, this non-goal information appeared even less prominent (in terms of neuronal modulation) than the irrelevant information concerning the previous goal chosen. To summarize, from these experiments, it emerges that the PFd can have a critical role in encoding and maintaining in memory a goal, both past and future, even when that memory is irrelevant.

Representing past goals in combination with outcome information, even when irrelevant, can reflect an output monitoring function, as suggested in §3. Furthermore, monitoring past goals could help to discover in the current context new contingencies and relationships between events that could lead to future decisions. For example, in the distance discrimination task [56,76], if the task contingencies changed suddenly such that the goal began to be located always to the right, discerning that the current spatial goal is on the right as in the past one could promote the switching to a much less cognitive demanding strategy, such as always choosing the right goal, instead of computing which goal is farther from the centre. Alternatively, monitoring the previous goal could simply be useful for confirming the validity of the current behavioural rule.

Previous studies have shown that the PFd can generate higher order representations or categories of movement sequences that extend beyond the representation of specific sequences of movements [79]. Such categories might be built by monitoring the relationship between different sequences of actions, although in this task [79] also generating such a higher order of categorical representation was not a task requirement. The slow-learning mechanisms of the PF cortex, in conjunction with the fast-learning mechanisms of the hippocampus and striatum [80], could facilitate the search for regularities among simple representations in the process of building an abstract representation of the task structure (see [81] in this issue).

Therefore, in a predictable environment, goal monitoring, even when monitoring is irrelevant to the task at hand, could help to search for better solutions to a problem. These potential solutions include helping to discover strategies that can speed-up learning, such as the repeat-stay or the change-shift strategies in conditional motor learning paradigms [7]. In the context of the classic exploration/exploitation trade-off, in which the PF cortex is thought to play an important role that adds new computational capabilities that go beyond reinforcement learning (see [82] in this issue), goal monitoring could be important during the exploration of new options [73]. Indeed, exploration should complement the tendency to exploit actions that lead to reward.

A recent study that compared the neural activities in several frontal and parietal areas using a matching pennies task that encouraged exploration with that of a visual search task that instead favoured exploitation showed that SEF neurons more profoundly enhanced previous goal signals during the exploratory task compared with the exploitation task. Moreover, this enhancement reflected the tendency to switch choices, suggesting a specific role for this area, but not the PFd (at least in this task), in explorative behaviour [61].

5. Conclusion

We have presented recent evidence that previous experiences can affect both behaviour and neural activity in several tasks. In motor-related areas (e.g. the FEF and PM), such tasks as the antisaccade and countermanding tasks have been used to demonstrate a neural correlate of proactive control with motor planning. In the hierarchically higher PFd cortex, tasks have mostly been used to explore memory encoding for the goals of previous trials. Currently available data suggest that previous goal and outcome information can affect neural activity in the PFd in the following contexts: (i) during associative learning [9]; (ii) when the current choice depends on the previous choice [7,11]; (iii) during value updating [72]; and (iv) in the context of a general monitoring function, even when past choices are irrelevant to the task performance [76]. Future studies should compare the roles of same versus different cortical and subcortical areas in adopting the same task, in order to understand the specific role that previous trial signals can play in each area.

References

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