EXPLORING THE CONSEQUENCES OF THE PREVIOUS TRIAL

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In tasks that are designed to explore cognitive functioning, the response on each trial is a function of the combination of experimental conditions that occurred on that and the previous trial. Because the previous trial influences performance, the event presented during or the action required by the previous trial must leave an imprint on the brain's activity that carries through to the next trial. These imprints are manifest in the activity of single neurons that participate in producing the response. Previous trial effects address disparate cognitive phenomena, such as response priming, task switching and inhibition of return, and the neural bases of previous trial effects can be envisioned as changes in salience of the target or the goal of the action on a spatial map.

TASK SET
The same stimulus (for example, a ringing phone) can produce different responses (lift versus do not lift receiver) depending on the situation (your office versus someone else's). Task set refers to the way of responding that is adopted in a given situation. Task-switching experiments measure the costs involved when switching between sets.

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Imagine flipping through a photograph album. A lot of information is contained in each picture. For instance, it is possible to guess the approximate age of the photograph on the basis of the clothing and hairstyles worn by the people posing for the shot, and the purpose of the gathering when appropriate props are included in the picture. All of this information can be gathered from a single picture because pictures accurately capture one instant in time.

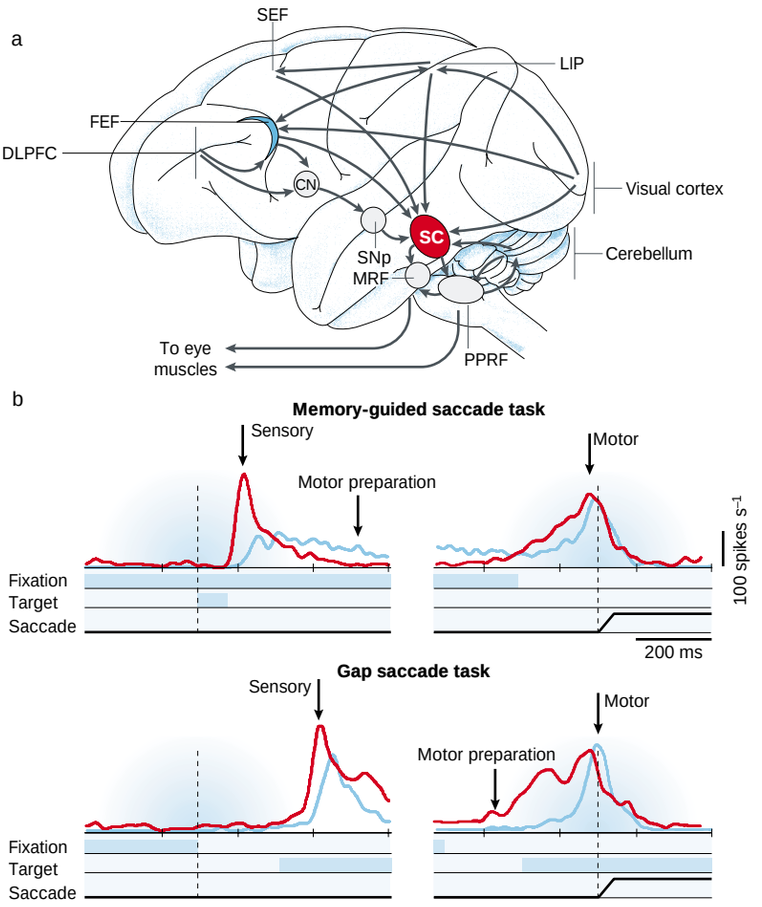
Knowing what happened at one instant cannot disclose how that moment came into being, though. For instance, a picture depicting a man, sleeping in a chair, while wearing a tuxedo, makeup and a tiara indicates that he was the target of a prank after he had too much to drink. However, from this picture we cannot know who the prankster was or whether alcohol was involved.

Many studies of human perception and cognition are conceptually similar to looking at single photographs. Consider a typical reaction-time study. The amount of time that is required to respond to a stimulus is compared between at least two conditions. When systematic differences in reaction time are obtained, the condition that evokes shorter reaction times is thought to require fewer steps or computations, or to involve more efficient processes, than the condition that evokes longer reaction times[1–5]. To provide an accurate representation of the conditions under study, each condition is tested several times, which assures a stable estimate of reaction time, and different conditions are presented in random order, which excludes systematic ordering effects. Even though each condition is sampled several times, this tactic is still equivalent to taking a single picture because all of the information that was obtained for each condition is blended into one instance, making it impossible to assess whether preceding events influenced the outcome of each trial.

Does the previous trial influence responding on the next trial? To answer this question, researchers compare the outcome of each trial on the basis of the trial that preceded it. Doing so shows that the conditions on the previous trial can increase or decrease response time, and can alter the trajectory of the response, depending on the task and circumstances. When reported, these previous trial effects have been interpreted as the consequences of priming[6–15], procedural learning[8,16], maintaining or switching TASK SET[17–20], attention[21–25], guessing strategies[26,27] or competing motor programs[28]. Despite these differences in tasks and interpretations, a common theme remains — preceding events modify performance.

Observing previous trial effects in behaviour indicates that information presented during, or the actions required by, the previous trial leave a residual imprint on the brain that carries through to the next trial. To find out how these imprints are manifest, the activity of single neurons is monitored while monkeys perform cognitive tasks that generate previous trial effects.

Box 1 | Saccadic eye movements and oculomotor neurophysiology



Saccadic eye movements are the response of choice in experiments involving non-human primates because they are simple, stereotyped actions for which the neuroanatomical substrates have been established[90–97] (a simplified version is shown in part a) and because the neurophysiological characteristics of the neurons in several of these structures have been described[92–98].

In the studies discussed in this review, neurons in the superior colliculus (SC) and frontal eye fields (FEF) were monitored while monkeys generated saccades to visual targets. Part b shows spike-density waveforms from visuomotor neurons in the superior colliculus (red) and frontal eye fields (blue) for a memory-guided saccade task (upper panel; a target is presented and extinguished, and the monkey initiates a saccade to the remembered location of the target) and a gap saccade task (lower panel; the fixation light disappears for 200 ms before the target appears). Both neurons show two peaks of activity. The first is a sensory signal that begins 50–100 ms after the target appears and that occurs even when a saccade is not generated[95,99]. The second is a motor signal that precedes the initiation of the saccade by 10–20 ms[95,100] and that appears only when a saccade is about to be generated[101,102]. The strength of the motor burst in the superior colliculus is related to saccadic velocity[103,104].

Two other cognitive signals can be seen in these tasks (or after small modifications to the tasks). Motor preparation is represented as low-frequency tonic activity during the trial, which increases when monkeys prepare to make a saccade into the neuron's response field[32] when they expect the target to appear at that position[30,33], when they covertly attend to that location[105], or when they choose to initiate a saccade to that location[106]. This increased low-frequency activity has been interpreted as motor preparation because the monkeys plan to initiate a saccade to the target's location in every example. Target selection is the second cognitive signal that is observed in the frontal eye fields[43–45] and superior colliculus[41], and is discussed further in the section on visual search.

CN, caudate nucleus; DLPFC, dorsolateral prefrontal cortex; LIP, lateral intraparietal cortex; MRF, medullary reticular formation; PPRF, paramedian pontine reticular formation; SEF, supplementary eye fields; SNp, substantia nigra pars reticulata.

Arranging neurophysiological data in chronological order and correlating these changes in the neurons' activity with the changes in behaviour shows how the previous trial exerted its influence.

Here, we describe the neurophysiological bases of previous trial effects. Each of the studies discussed has reported different behavioural consequences of the previous trial. All of these studies have used oculomotor tasks and have monitored the activity of oculomotor neurons in the frontal eye fields and superior colliculus. For readers not familiar with the oculomotor system, BOX 1 describes why saccadic eye movements are the response of choice in many non-human primate experiments, and it summarizes the basic neural signatures that correspond to sensory, motor and cognitive processes. In BOX 2, we introduce the concept of a salience map, which provides a simple and effective way to envision the influence of the previous trial on spatial maps that are similar to those of the frontal eye fields and superior colliculus. We begin by describing the simplest example of previous trial effects that have been documented — those observed during a two-alternative choice reaction-time task.

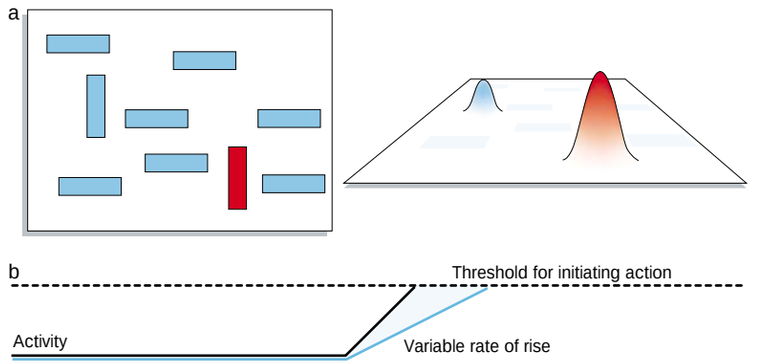
Two-alternative choice tasks

In the two-alternative choice SACCADE task, monkeys generate a saccade to a visual target that appears to the left or right of the centre. The absolute location of the target (left versus right) has little influence on performance. However, the relative location of the target does have an influence: saccadic reaction times are faster when consecutive targets appear at the same location than when they appear at different locations[29] (FIG. 1a).

How is this repetition advantage expressed in the activity of single neurons? FIGURE 1b shows that the activity of a neuron was elevated (arrow) before the target was registered by the neuron when the previous trial was generated to the same location (in blue) compared with when it was generated to the opposite location[30,31] (in red). This increase in pre-target activity, which was observed across the population of neurons in this study (FIG. 1c, right), shortens saccadic reaction time by allowing the threshold of activity for generating a saccade to be reached sooner (FIG. 1c, left). In support of this notion, the magnitude of pre-target activity predicts saccadic reaction times on a trial-by-trial basis: increased pre-target activity is associated with shorter saccadic reaction times[30] (FIG. 1d; individual neuron, left; population, right).

In other words, the repetition advantage in saccadic reaction times occurs when elevated pre-target activity increases the salience of a localized region on the saccadic map, which brings this region closer to threshold for initiating a saccade (BOX 2). Although this study shows a clear-cut relationship between behaviour and neural activity, two issues remain unexplained. First, we do not know what is responsible for the elevated pre-target activity. In previous studies, increased pre-target activity has been associated with motor preparation[32,33]. However, there is no reason for monkeys to anticipate a repeated action when the target is equally likely to appear at either side. Indeed, manipulating the likelihood

Box 2 | Salience maps in the frontal eye fields and superior colliculus



The salience map, which is often used in computational models of attentional shifting[77–79], is a useful concept for this article because it provides a simple way to envision changes in neural activity that are associated with the previous trial. A salience map is a two-dimensional, topographically organized map that represents the distinctiveness of objects in the visual scene. This map can be modified, or tuned, by the goals of the observer[78].

This concept is illustrated in part **a**. Two salient objects are presented in the visual scene (left): a red vertical bar and a blue vertical bar among blue horizontal bars. In response to this scene, two peaks of activity (represented by bumps) occur on the salience map (right). The red bar results in a greater level of activity because it differs from other objects in the scene in two ways (colour and orientation), whereas the blue vertical bar differs from the other objects only in orientation. The region with the highest level of activity is chosen as the next target of attention.

The frontal eye fields[107] and the superior colliculus[40] share several key features with this theoretical salience map[108–110]. The neural activity that is linked to visual objects represents the salience of these objects in the overall level of activity elicited by the presentation of the object and in how quickly the sensory response discriminates among the objects[37,66,107]. Also, the goal of the participant influences the representation of these objects, as the expectation or importance of the object modulates its sensory response[29,33,111,112].

How the salience map links to motor behaviour is an interesting and important issue. Under most circumstances, the neurophysiological correlates of salience closely match saccadic behaviour[37,66,107,113]. The same neurons in the superior colliculus (visuomotor neurons) encode both the salience of the object and any subsequent saccade directed to that object[41]. By contrast, salience and motor programming can be dissociated in visual neurons in the frontal eye fields[107,114]. Perhaps neurons that encode both signals link salience with motor programming.

A simple way to connect salience mapping and motor programming is through the variable rise-to-threshold model[115] (**b**). In this model, activity accumulates at different rates (blue and black lines) towards a fixed threshold (dotted). Variability in achieving threshold (shaded region) is responsible for the differences in reaction times that are observed in behaviour. If there are competing programs, the one that reaches threshold first produces the motor action.

that a target will appear on one side increases pre-target activity further[30]. So, we do not have a good explanation for this effect. Second, we do not know why monkeys show a repetition advantage but humans produce an alternation advantage when tested in the same way[34] (see also REFS 23–27). Practice might be an important factor in producing this species difference, because humans are typically naive when they participate in such experiments, whereas monkeys can perform thousands of trials a day, five days a week, for many months. Indeed, sufficient practice eventually eliminates the alternation advantage in human participants[35]; perhaps after even more practice, a repetition advantage would emerge in its place.

SACCADE
A rapid eye movement (with speeds of up to 800° s^{-1}) that brings the point of maximal visual acuity — the fovea — to the image of interest.

Visual search

In the last example, we described previous trial effects that occur reliably in single-cell activity when a simple two-alternative choice saccade task is implemented. Most studies that explore human cognition include more than two potential targets, making it important to assess previous trial effects in more complex tasks. For example, in the oddball localization task, an array of visual objects is presented to an observer who must generate a saccade to the odd one[36–44] (see also REFS 7,10–13). In the studies described here, the colour of the search items differentiated the target from the distractors, which were red or blue (FIG. 2a) (other feature differences such as shape[37] and gradients[10] produce similar previous trial effects). The colour that identified the target and the target's location were selected randomly across consecutive trials. Comparing saccadic reaction times for each variable showed that neither the absolute colour (red versus blue) nor the absolute location of the target influenced performance. However, previous trial effects were obtained: two originating from the colour of the target (same versus different target colour) and one originating from the location of the target (same versus different target location).

Colour of the target. The colour of the target across consecutive trials produces two distinct previous trial effects: priming of pop-out when the target colour remains the same, and competing motor plans when the target colour changes. After describing the neurophysiological correlates of these phenomena, we propose that both effects represent different perspectives of the same picture.

When performing the oddball localization task, monkeys respond faster and make fewer errors when the colour of the target remains the same across consecutive trials[37] (FIG. 2b). Humans show the same effect, which is called priming of pop-out[7,10,42].

In the frontal eye fields, priming of pop-out is represented in the neural signature that is linked to target selection. In response to the appearance of the search array, the activity of visual neurons in the frontal eye fields increases. At first, the magnitude of a neuron's activity is similar whether the target or a distractor is in its receptive field. Shortly thereafter, the neuron increases its activity when the target is in its receptive field, but decreases its activity when a distractor is in its receptive field[43–45] (target selection). The colour of the target on the previous trial affects how quickly target selection is achieved: it is faster when the colour of the search array remains the same across consecutive trials (FIG. 2c; top panel, blue trace) than when it changes (bottom panel, red trace). This difference becomes larger as the number of repeated trials increases[38] (FIG. 2d, behaviour; FIG. 2e, neural activity).

When the colour relationship changes across trials, monkeys make more short-latency corrective saccades and the trajectories of single saccades are often curved. Both of these effects have been interpreted as evidence for concurrent programming of saccadic motor plans. Short-latency corrective saccades (FIG. 3c) occur when

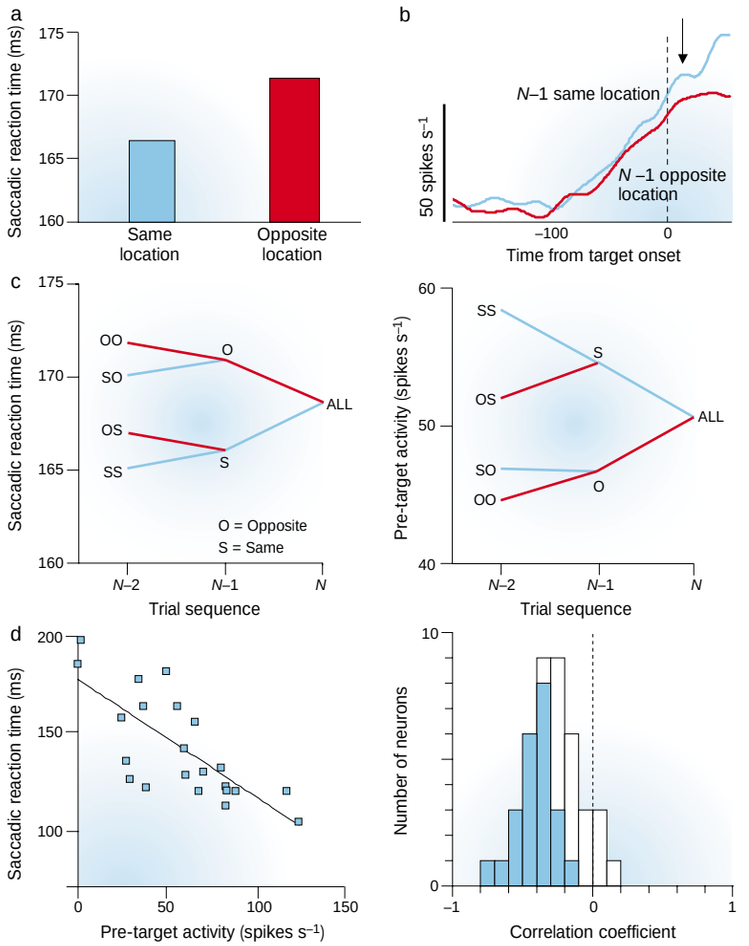


Figure 1 | **The two-alternative choice saccade task. a** | Average saccadic reaction times in the two-alternative choice saccade task when the targets appeared at the same or the opposite location as the previous trial. **b** | Averaged spike-density waveforms of a visuomotor neuron in the intermediate layers of the superior colliculus, showing pre-target activity when the target in the previous trial appeared in the response field of the neuron (blue) or at the opposite position (red). **c** | Previous trial effects accumulate across multiple consecutive trials. Saccadic reaction times continue to decrease as the number of repeated trials increases (left) and this further decrease in saccadic reaction time is associated with further increases in pre-target activity (right). *N*, current trial; *N*–1, one trial back; *N*–2, two trials back. **d** | Left, correlation between saccadic reaction time and pre-target activity for a single neuron; right, distribution of correlation coefficients between pre-target activity and saccadic reaction times for every neuron in the sample. Blue bars represent correlations that achieved statistical significance ($p < 0.05$). ALL, all locations.

the participant initiates a saccade towards the distractor before initiating a second saccade to the target. The important feature of the second, corrective saccade is that it must have been programmed at the same time as the first saccade because its reaction time is shorter than the theoretical minimum time that is required to plan and initiate a saccade[39,40,42] (see also REFS 46–48). By contrast, curved saccades are single saccades that do not follow a straight trajectory, but that are arched. In visual search, these curved saccades are rare, but they occur most frequently when monkeys incorrectly generate a saccade to a distractor. In this case, the saccade's trajectory bends towards the target[39,49] (see also REFS 50–53) (FIG. 3d).

The distinct patterns of neural activity associated with concurrent programming of saccadic goals are shown in FIG. 3. FIGURE 3a shows the activity of a neuron when the target appears in its response field and a straight saccade was initiated to its location. There is one distinct burst, corresponding to motor-related activity. FIGURE 3b represents the activity of the same neuron when a straight saccade was initiated to a target adjacent to its response field. In this instance, there is no motor burst because the saccade was not initiated into the response field of the neuron. Compare these examples, in which the associated behaviour showed no concurrent saccadic plans, with instances in which it did (to facilitate these comparisons, the activity shown in FIG. 3b is reproduced). FIGURE 3c shows the activity of the same neuron when a second, short-latency saccade was directed to the target (inside the neuron's response field) after the first saccade was initiated to a distractor (outside the neuron's response field). In this case, the activity of the neuron encoding the goal of the second saccade was elevated when the first saccade was initiated (red trace), indicating that a competing motor plan was present. A similar elevated response was seen when the trajectory of the saccade (directed elsewhere) was curved towards the target (inside the neuron's response field) (FIG. 3d, blue trace). In support of the idea that competing motor programs cause curved saccades, artificially inducing a competing motor program through electrical stimulation produces saccades with trajectories that are bent towards the site of stimulation[49].

So, whether the colour of the target changes from trial to trial has important consequences. When it remains the same, participants initiate a response faster and this priming of pop-out is associated with faster target selection in the frontal eye fields[37]. When it changes, participants produce responses that indicate that competing motor programs were planned, and these concurrent motor programs are seen in the salience maps of the superior colliculus[40,49].

Up to now, these previous trial effects have been treated separately. However, priming of pop-out and concurrent motor programs might represent different aspects of the same picture; that is, differences in the relative salience of the target that originate from maintaining or switching task set[17–20]. The colour that defines the target on half of the trials defines the distractors on the remaining trials, because the colour of the target (and distractors) is selected randomly and only two colours are used (short runs of trials in which the target's feature remains the same have been used in some studies[37]). Even though participants can flexibly choose which object is the target on each trial, it is easier for them to make this decision when the colour does not change (maintaining task set) than when it does change (switching task set). So, when the colour of the target remains the same across consecutive trials, the target's salience increases and the distractors' salience decreases, which allows participants to respond more efficiently. Consistent with this explanation, the advantage of keeping the colour the same grows as the number of trials increases[10,37] (FIG. 2d,e), and this is associated with an increasingly exaggerated neural representation of the

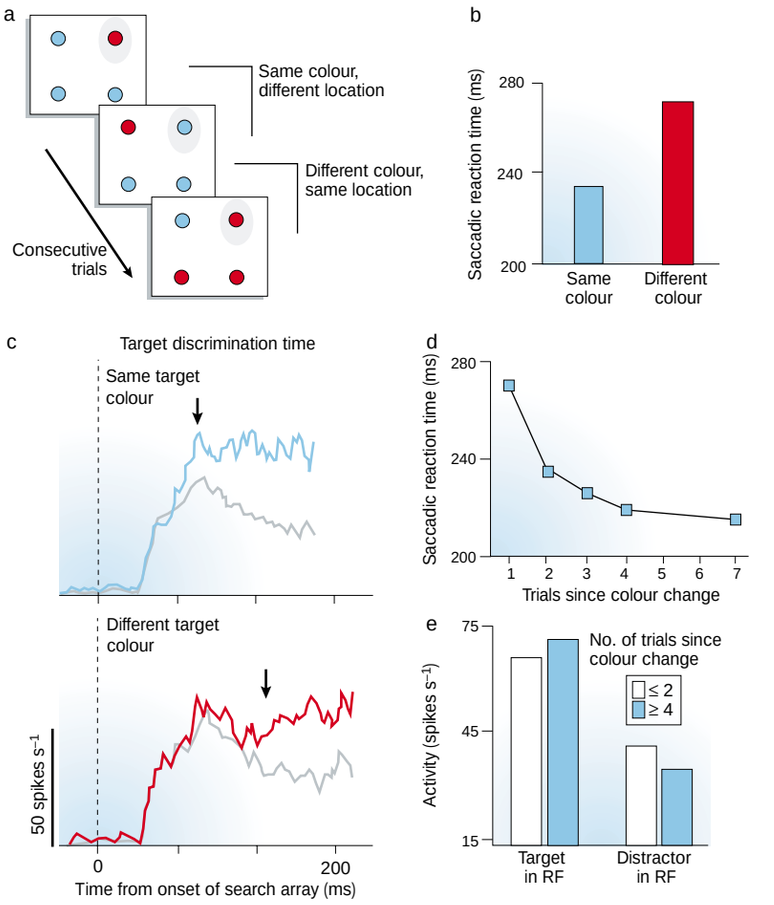


Figure 2 | **The oddball localization task. a** | Illustration of the task. In the second search array, the colour of the target is the same as in the first, but the location has changed; in the third array the location of the target remains the same, but the colour has changed. Grey ellipses represent a neuron's response field. **b** | Average saccadic reaction times when the colour of the target remained the same (blue) or changed (red) across consecutive trials. **c** | Averaged spike density waveforms of a single neuron in the frontal eye fields, showing previous trial effects when the colour of the target remained the same across consecutive trials (top) and when it changed (bottom). Arrows show differences in target discrimination time. Grey lines show activity when a distractor was in the neuron's response field (RF). **d**,**e** | Changes in saccadic reaction time (**d**) and neural activity (**e**) as the number of trials across which the target colour stays the same increases. Modified, with permission, from REF. 37 © (2002) Society for Neuroscience.

target and increasingly attenuated neural representations of the distractors in the frontal eye fields[37]. A similar pattern of improvement has been obtained in task-switching studies[17,18]. Alternatively, when the colour of the target changes across consecutive trials, the salience of the distractors is accentuated because the same feature defined the target on the previous trial, which causes the distractors to compete with the target for selection[28]. Consistent with this explanation, allowing participants to maintain the same task set eliminates the interference of a distractor in a variant of the oddball search task[54]. Viewing priming of pop-out and concurrent motor plans as changes in the relative salience of the target that originate from maintaining or switching task set provides a succinct way to explain the different effects that arise from the colour of the target on the previous trial.

Location of the target. Changing the location of the target across consecutive trials also produces previous trial effects. Monkeys respond more slowly when the target appears at the same location as in the previous trial than when it appears at a different location[37] (FIG. 4a). In the frontal eye fields, this change in behaviour is reflected in delayed target selection when consecutive targets appear in the same position (FIG. 4b). Bichot and Schall[37] interpreted this location-based slowing as inhibition of return, consistent with previous empirical findings and theoretical developments[23–25,55–57].

Inhibition of return describes the tendency of observers to be slower to reorient to a previously attended location than to orient to a new location[58–60], which encourages them to explore new locations in their environment[56]. In addition to its important role in orienting spatial attention, inhibition of return provides us with the opportunity to explore the consequences of the previous event (rather than the previous action) by using a cue–target task instead of the oddball search task. In this task, the 'previous trial' is replaced by a cue to which no response is required. Each trial begins with participants maintaining their gaze at a central location (FIG. 5a). A brief flash of light (the cue) then appears at one location in the visual periphery, followed by a second visual object, the target, appearing at either the same or a different location. In many studies, participants indicate the spatial location at which the target appeared, either with a manual button press (for example, left button press for left target) or by initiating a saccade to the target's location[60,61]. When the time between the onset of the cue and target exceeds ~200 ms, and the cue does not predict the upcoming location of the target, participants respond more slowly when the cue and target appear at the same location[56,62] than when they appear at different locations. Therefore, the appearance of a cue alone is sufficient to produce inhibition of return.

What influence does the cue have? FIGURE 5b shows the activity of a single neuron in the superior colliculus during this task. When the target appears in the neuron's response field and the cue appears to the opposite side (red line), two peaks of activity occur, the first representing the sensory response to the target (hereafter referred to as target-related) and the second representing the motor burst that precedes the saccade. By contrast, when both the cue and the target appear in the neuron's response field (blue line) there are three peaks of activity: the first peak represents the sensory response to the cue, the second the sensory response to the target, and the third the motor burst. Comparing these conditions reveals two consequences of the cue when it appears on the same side as the target: the firing rate of the neuron is elevated immediately after the cue (arrow) and the target-related response is attenuated (highlighted with the yellow bar). These are conflicting signals; the elevated firing rate between the cue and the target indicates that the neuron is more excitable[30,33,63] but the attenuated target-related activity indicates that the neuron is receiving a weaker incoming visual signal (see REFS 64,65 for similar findings in the superficial

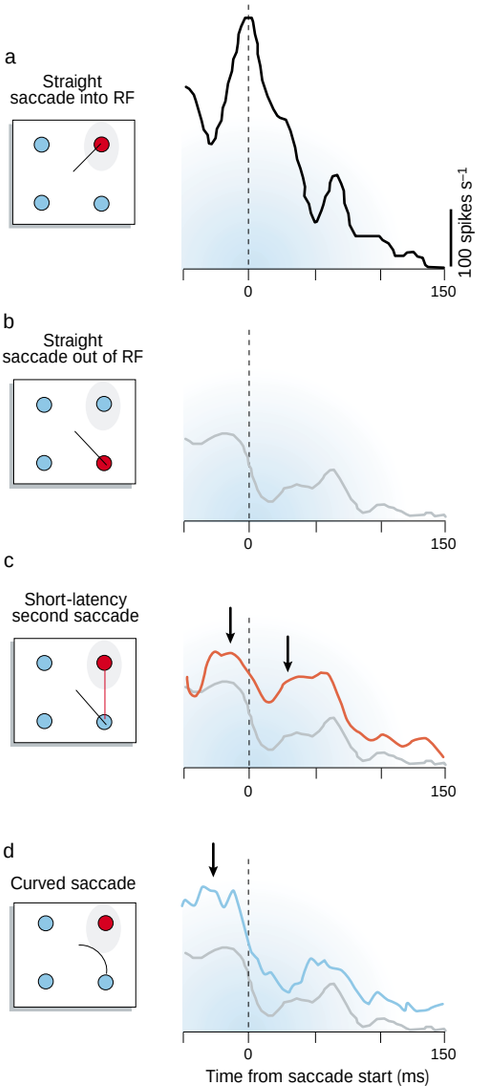


Figure 3 | **Competing motor plans. a**,**b** | Behavioural and neural correlates of trials when no concurrent motor plans were observed. A single straight saccade is generated into the response field (RF, grey ellipse) of the neuron (**a**, black line) or to the adjacent location outside the neuron's response field (**b**, grey line). **c**,**d** | Behavioural and neural correlates of trials when concurrent motor plans were observed. **c** | Short-latency second saccades, in which the second concurrently programmed saccade was initiated into the response field of the neuron (red line). **d** | Curved saccades with the trajectory bent towards the response field of the neuron (blue line). Arrows indicate the elevated neural activity associated with the concurrent motor plan. The grey line in **c** and **d** is reproduced from **b** for comparison. Modified, with permission, from REFS 40,49 © (2002) The American Physiological Society.

SPATIAL REFERENCE FRAMES
A reference frame describes a set of coordinates that is used to define where an object is located in space. In a retinocentric reference frame objects are mapped in retinal coordinates. In an environmental based (or allocentric) reference frame objects are mapped in world-based coordinates.

layers of the superior colliculus and posterior parietal cortex). In the face of these conflicting signals, the monkeys respond more slowly when the cue and target appear at the same location, which indicates that the target-related activity dominates the behaviour. This outcome makes sense because the target-related signal is the last signal received before the action is initiated (participants initiate a saccade when the target appears) and, therefore, is crucial in allowing the neuron to reach threshold activity for the motor action (BOX 2). Consistent with this interpretation, target-related activity correlates closely with saccadic reaction times on a trial-by-trial basis (less activity is associated with slower response times[66]). Saccadic reaction times do not show a similar relationship with the elevated activity before the target[67].

Comparing the neurophysiological correlates of inhibition of return that originate from visual search (delayed target selection) and from the cue-target task (attenuated target-related activity) shows that the neurophysiological mechanisms responsible for inhibition of return might differ depending on the task used to produce it. This is not an unexpected finding, as there is accumulating behavioural evidence that inhibition of return might originate from many mechanisms, because small changes to the cue–target task modify its characteristics. For instance, asking participants to respond with different effectors (eye versus hand) changes the amount of time between cue and target that is needed to produce inhibition of return[60,68] and the SPATIAL REFERENCE FRAME in which inhibition of return is encoded (retinocentric versus environmental[69]; see also REFS 70–72). Even when effector differences are disregarded, changing whether participants detect the onset of the target or indicate a feature of the target (such as its colour) also changes when inhibition of return is observed[73] and, in some instances, can change whether inhibition of return occurs at all[23–25]. Clearly, much research is required before we fully understand the mechanisms of inhibition of return and we should be cautious in extending findings between studies.

Focusing on the differences across studies ignores one feature that is common to both of the physiological examples — inhibition of return originates from the diminished salience of the target (even though it is caused by different mechanisms). Although this does not explain all facets of inhibition of return[74–76], it is consistent with computational models of attention, which propose that inhibition of return decreases the salience of the object and allows new locations in the visual world to be explored[77–79].

Conclusions

As we have shown, previous trial effects can be produced in various tasks and can originate from different neurophysiological mechanisms. One simple way to integrate these different effects is to consider how the previous trial changes the salience of the target, or the goal of the action, on a spatial map (BOX 2). In all instances, the target's representation is modified by the previous trial, increasing or decreasing its representation on the salience maps of the frontal eye fields or superior colliculus.

Consider first the repetition advantage in the two-alternative choice saccade task. In this instance, increased pre-target activity of neurons in the superior colliculus enhances the relative salience of that region

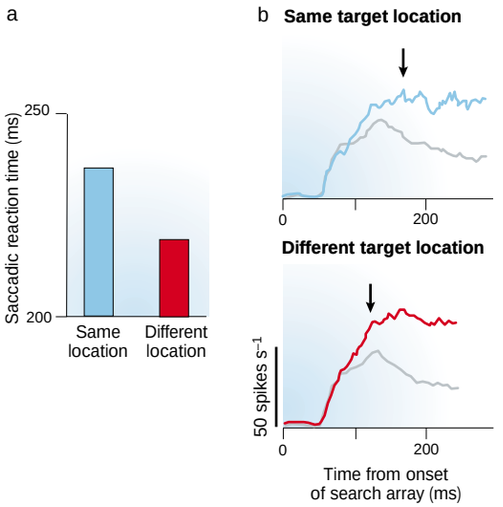


Figure 4 | **Effects of target location in a visual search task. a** | Average saccadic reaction time when the target remained at the same location and when it changed location from the previous trial. **b** | Averaged spike-density waveforms of visual neurons in the frontal eye fields that show differences in target selection when the consecutive target appeared at the same location (top panel, blue) and when they appeared at different locations (bottom panel, red). Arrows indicate differences in target discrimination time and the grey lines show activity when the target was not in the neuron's response field. Modified, with permission, from REF. 37 © (2002) Society for Neuroscience.

on the map, which allows the saccade to be initiated faster when the target appears at that location. Likewise, priming of pop-out and competing motor plans might reflect the relative saliences of the target and distractors. When the salience of the target is high and the salience of the distractors is low because participants have maintained the task set, priming of pop-out is produced. By contrast, when the salience of the target is low and the salience of the distractors is high because participants have switched task set, the distractors compete with the target and can influence the trajectory of the saccade or result in the rapid initiation of a second saccade. Finally, inhibition of return originates from delayed target selection or from attenuated target-related activity, depending on the task used to produce it, which causes the salience of the target to be lower. Because the target drives the motor plan in all of the tasks described in this review, modifications of the salience of the target alter how quickly threshold for achieving an action can be achieved and produce the changes in behaviour that we associate with previous trial effects.

This review does not describe all previous trial effects that have been reported. By focusing on the neurophysiological correlates of previous trial effects in oculomotor structures, we have not shown why the extrinsic inputs into these structures have been modified. For instance, the attenuated target-related processing in inhibition of return is seen early in sensory processing, for example in the superficial layers of the superior colliculus that receive inputs from the retina and early visual areas[64,66]. Similar attenuated processing of visual objects has been observed in brain structures that are more closely tied to visual perception: for instance, previous exposure to a visual object decreases its neural representation in inferior temporal neurons the next time it is presented[80–83] (see also REFS 84–86). How this change in neural activity translates into behaviour is unclear. It might be responsible for repetition priming (the tendency to respond faster to an object when it is repeated[82,87–89]) or for negative priming (the tendency to respond more slowly to an object when it is repeated[9,14,15]). Perhaps the parameters of the task used to explore previous events change the way the same signal is translated in the salience maps[23–25]. This is an open question for future research.

Returning to the analogy described in the introduction, a single picture accurately captures one instant, but does not reveal the events involved in shaping that moment. For instance, our friend wearing lipstick and the tiara was not entirely responsible for his unusual appearance. Like single photographs, cognitive processes are also influenced by previous events, in which participants might respond more quickly or slowly, or the trajectory of the response might be altered. We have discussed how these changes in behaviour are reflected in the activity of single neurons in the salience maps of the frontal eye fields and superior colliculus, wherein the previous trial increases or decreases the salience of the target. Our goal was to review examples of previous trial effects in the oculomotor system, to show that the neural imprints involved in producing these previous trial effects can be reliably measured, and to stimulate further research in this area. Ultimately, history might prove this review to be preliminary in its content. Even so, it cannot undo one clear concept summarized in this article — preceding events or actions shape the outcome of each trial and these previous trial effects can be reliably observed in the activity of single neurons that are involved in encoding the response.

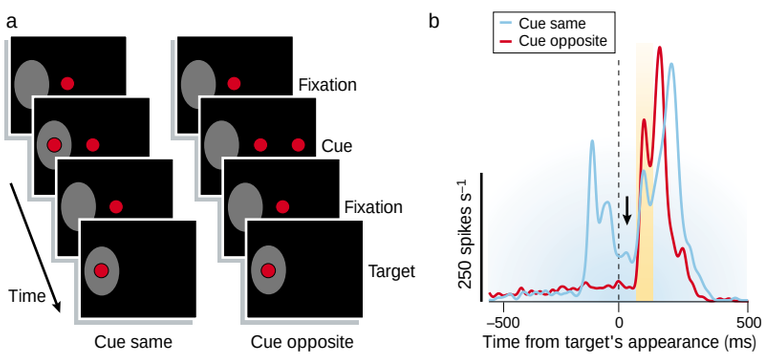


Figure 5 | **Inhibition of return. a** | Design of a cue–target task used to explore inhibition of return. Grey ellipses represent a neuron's response field. **b** | Averaged spike-density waveform of a visuomotor neuron in the superior colliculus, revealing the attenuated target-related response (shaded in yellow) when the cue appeared at the same location as in the previous trial (in blue) compared with when it appeared in a different location (in red).

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