



Research report

Short-term motor plasticity revealed in a visuomotor decision-making task

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ABSTRACT

Selecting and executing an action toward only one object in our complex environments presents the visuomotor system with a significant challenge. To overcome this problem, the motor system is thought to simultaneously encode multiple motor plans, which then compete for selection. The decision between motor plans is influenced both by incoming sensory information and previous experience—which itself is comprised of long-term (e.g. weeks, months) and recent (seconds, minutes, hours) information. In this study, we were interested in how the recent trial-to-trial visuomotor experience would be factored into upcoming movement decisions made between competing potential targets. To this aim, we used a unique rapid reaching task to investigate how reach trajectories would be spatially influenced by previous decisions. Our task required subjects to initiate speeded reaches toward multiple potential targets before one was cued in-flight. A novel statistical analysis of the reach trajectories revealed that in cases of target uncertainty, subjects initiated a spatially averaged trajectory toward the midpoint of potential target locations before correcting to the selected target location. Interestingly, when the same target location was consecutively cued, reaches were biased toward that location on the next trial and this effect accumulated across trials. Beyond providing supporting evidence that potential reach locations are encoded and compete in parallel, our results strongly suggest that this motor competition is biased by recent trial history.

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1. Introduction

Among the most challenging problems faced by our visuomotor system is the selection of targets in a cluttered world filled with many objects that could be acted upon. One possible solution to this problem is revealed by neurophysiological studies that suggest the brain plans multiple motor programs in parallel [1–5], allowing for several targets to compete for action selection at any one time. This strategy facilitates and simplifies target selection. Because all the potential actions are simultaneously coded, selection of the final action becomes the more straightforward process of one action plan ‘winning out’ over the others. This motor competition requires that each potential plan be associated with levels of activation reflecting its likelihood of being selected [e.g. [1]], but it is rather poorly understood what specific target and task properties modulate this competitive process.

In a recent experiment, we found that when subjects performed rapid reaches toward two equally likely targets *before* one target was cued in-flight, subjects initiated a ‘spatially’ averaged trajectory toward the midpoint of the potential target locations [6]. This is consistent with other eye-movement and reach paradigms demonstrating that movements made in the presence of competing stimuli tend to deviate between the stimulus locations [7–10]. In a second experiment, we also showed that reach trajectories were biased both by the spatial location of the potential targets and by the number of targets on each side of space, suggesting that location and probability are factors that influence motor plan competition [6]. This pattern of results, however, is consistent with the idea that all the potential targets (and actions) have identical weights. Yet it is necessary to have a visuomotor system that can independently adjust the weightings of each potential target and action. Indeed, motor decisions are based not only on the information currently available to the sensory system, but also on previous visuomotor experience [e.g. [11]]. Visuomotor experience and the changes associated with that experience can accrue over timescales of weeks or months [12,13] but can also be seen to operate over much shorter intervals [e.g. [9,14,15,16]]. Specifically, it has been shown that the parameters of a current movement are influenced by the characteristics and intentions of the previous movement. It

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is precisely this trial-to-trial motor plasticity that we investigated in the current experiment: how the selection of a given target on one trial alters its weighting in the competition between targets on the subsequent trial.

Trial history effects reveal how visuomotor decision-making processes evolve across multiple movements [e.g. [14,15,17,18]] and have been investigated in a wide range of paradigms. For example, subjects are faster to detect targets when the location is repeated [19], and grasping kinematics are affected by the recent availability of visual feedback [20,21]. Target-directed eye movements provide a particularly good illustration of the effects of trial history: the colour, shape and location of the target on a previous trial influences both the neural activity in eye-movement-related structures during motor planning and the subsequent behavioural response [e.g. [7,22,23]]. In addition, behavioural studies have shown that reach targets embedded among distractors that vary in colour from trial-to-trial produce more variable reach trajectories than targets that maintain a colour across trials [24]. Of particular relevance is recent work investigating the effects of previously performed arm movements on subsequently performed actions. For example, avoiding a virtual obstacle on one trial will result in a more curved trajectory on the next trial even when no obstacle is present [25,26]. These results suggest that successive movements in a sequence are not programmed *de novo* but instead are created by slightly modifying the blueprints of the preceding movement(s) [27]. In the current study, we wanted to capitalize on this proposed holdover of motor parameters from trial-to-trial as a way of creating a disparity in the weightings assigned to two potential targets. As such, we tested if the spatial averaging between potential targets that we have previously reported [6] would be biased toward the location of a previously cued target, and if so, whether this bias would accumulate across multiple trials.

2. Methods

We recorded rapid reach movements (OPTOTRAK, 150 Hz) from 17 right-handed (mean age 25.5 years, 10 female) subjects as they reached from a start button to a touch screen (40 cm away). Trials began with participants holding down the start button and fixating a cross centered on screen for a variable time ranging from 1000 to 2000 ms. A beep signalled when fixation was replaced by a target display, consisting of one or two outline targets (1-cm radius circle, black, on a white background), and also provided the cue for subjects to initiate a reach (within 325 ms). Upon button-release, one of the target(s) in the display was cued (filled-in black) and subjects had to correct their trajectory in-flight to that location (within 425 ms) [see Fig. 1A]. To ensure rapid and accurate movements, subjects received visual feedback about their performance at the center of the screen following each trial (to see a video of the task see [Supplemental Material](#) online). There were four possible types of errors each of which would cause a different line of text to be centrally displayed: *Too Early* (if the start button was released before 100 ms had elapsed), *Time Out* (if the start button was not released within 325 ms), *Too Slow* (if the screen was not touched within 425 ms of button-release), or *Miss* (if subjects did not touch within a 6 cm × 6 cm box centered on the target). *Good* was displayed on trials without errors. On *Too Early* and *Time Out* trials, the final target was never cued and the trial was removed and immediately repeated (9% of trials), preserving the sequencing (see below). For analysis, we removed only those trials with the slowest movement times (slowest 5% across all participants) as well as trials where participants missed the target (6%—for analysis of *Miss* errors, see [Supplemental Material](#)). After trial removal, two participants were excluded from analysis, failing to meet our criterion of at least four successful repetitions of each type of trial across the experiment (leaving 15 participants for statistical analyses).

The centers of the two potential targets were 9 cm to the left and right of fixation. Single-target trials served as a baseline since subjects knew in advance what the final location of the cued target would be. In two-target trials, prior to movement onset, subjects needed to prepare for either target to be cued. We embedded specific sequences of target-cueing across trials to test the effect of a previous trial on the next trial's movement, while ensuring that the left and right targets were cued equally often across the entire experiment. Each block of trials consisted of four repetitions of the sequence shown in Fig. 1B, which itself was composed of one repeat-left and one repeat-right micro-sequence. The direction (left or right) of the first micro-sequence in each block was determined randomly and alternated thereafter. The trials of interest within a micro-sequence consisted of the set of two-target 'Repetition' trials where the final target was consecutively cued on the same side of space. A 'Repetition' sequence contained two to five repeated trials (repetition

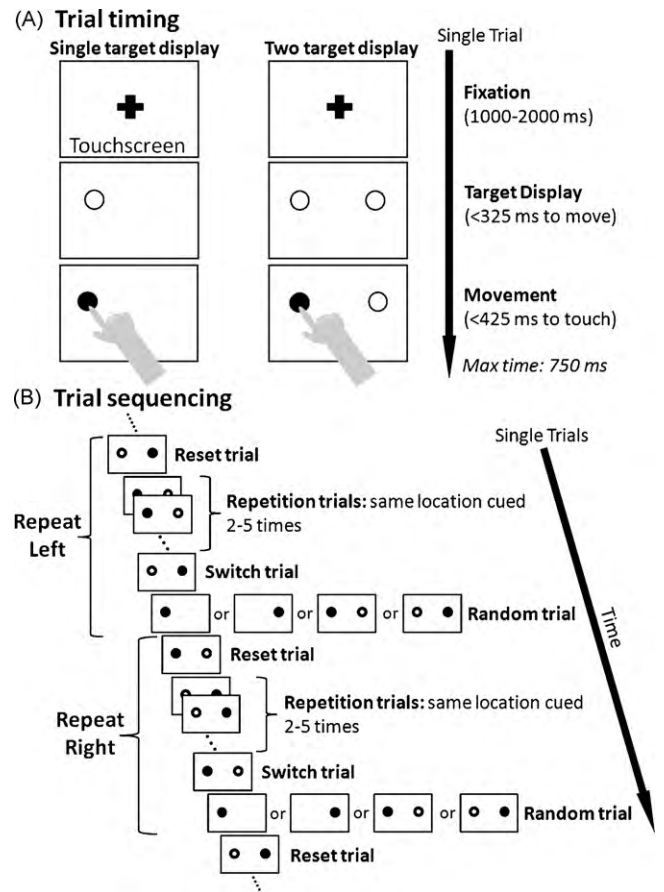


Fig. 1. (A) *Trial timing*: Trials began with the subject fixating a cross for a variable time interval (1000–2000 ms). This was followed by a target display containing one or two possible targets (shown schematically, size not to scale), which also provided the cue for subjects to initiate a reach to touch a target that would be filled in at movement onset. Upon presentation of the target display, subjects had 325 ms to lift their finger off the start button, and then an additional 425 ms to reach and touch the cued target. (B) *Trial sequencing*: Each repetition sequence consisted of one repeat-left and one repeat-right micro-sequence. Each micro-sequence began with a 'Reset' trial (target cued opposite to the upcoming Repetition trials) followed by 2–5 Repetition trials (target cued consecutively to one side), then a 'Switch' trial (target cued opposite preceding Repetition), and finally a 'Random' trial (target cued on either side in a single- or two-target display).

length selected randomly but presented only once per block, per side). To ensure that the participants were unaware of the repetition manipulation, and to mitigate the effects of trial repetition on a subsequent repeat sequence, we inserted trials before and after each set of 'Repetition' trials. Thus, each micro-sequence began with a 'Reset' trial in which the cued target was presented on the side opposite the upcoming Repetition sequence. Following the Repetition sequence, there was a 'Switch' trial where the target was cued on the side opposite the repeated sequence. Finally, following the 'Switch' trial, there was a 'Random' trial where the target could be cued on either side of space *and* could be either a two-target or single-target trial. Following the conclusion of one micro-sequence (e.g. repeat-left), a micro-sequence in the opposite direction was presented (e.g. repeat-right). Participants completed 10 blocks for a total of 540 trials. Each block began and ended with one additional randomly selected two-target trial to again ensure that participants were unaware of the sequence manipulation. Importantly, participants in post-experiment interviews never reported detecting any contrived patterns in trial sequencing.

3. Results

We employed functional data analysis techniques [28] to fit mathematical functions (using b-splines, see [Supplemental Material](#) and our previous work [6] for description of this technique) and to spatially normalize the reach trajectories. This enabled us to use functional analyses of variance (FANOVAs) to compare reaching behaviour across the conditions of interest. A

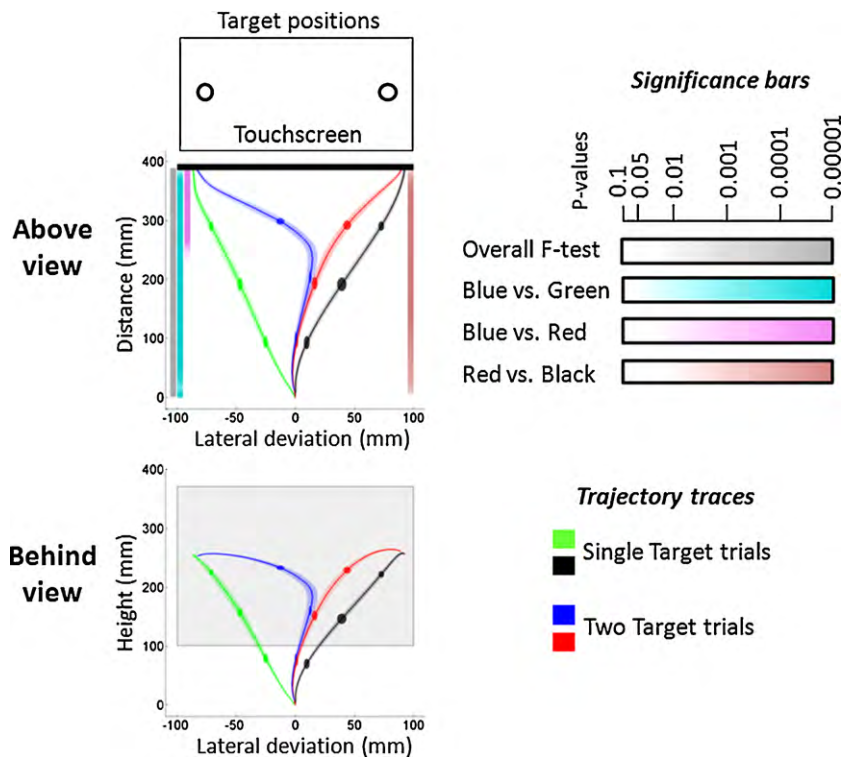


Fig. 2. Averaged three-dimensional reach trajectories from all Reset and Random trials shown from above (top-panel, x-axis is twice scale) and behind the participant (bottom-panel, x-axis is twice scale). Participants made reaches from a start button (0,0,0) to a touch screen located 40 cm away (denoted by thick black line and gray rectangle). Target displays contained either one (single-target trials, black- and green-traces) or two (two-target trials, blue- and red-traces) hollow circles. Coloured bands around trajectory traces represent average standard error across 15 participants with darkened spheres at 25%, 50% and 75% of reach distance proportional to the velocity in each dimension. Significance bars located in the top plot give a measure of where there were statistical differences between trajectories in the lateral dimensions, with the intensity of the bar-colour indicating the strength of significance (see legend). Target display (at the top) is not drawn to scale.

FANOVA is a statistically sensitive technique which extends a traditional univariate ANOVA (which is conventionally used to compare single points in time or space across curves) to all points in a curve, allowing a quantification of not only if, but also where and with what magnitude trajectories differ. This technique yields a comprehensive picture that is not available with a non-functional analysis. To report the regions where FANOVAs are significant, we use significance bars in which the intensity of the bar at each point in space denotes the magnitude of the significant difference for that comparison at that location.

We replicated the spatial averaging effect, we have reported previously [6] [see Fig. 2]. Reaches were made straight toward single targets (Fig. 2, black- and green-traces) but were initially aimed at the midpoint between the two targets on Random and Reset trials (red- and blue-traces), before correcting to the cued position in-flight. This was confirmed using a FANOVA (4-level repeated measures) comparing the lateral (x) deviation at different reach distances (y) across the single and two-target trajectories. The FANOVA was statistically significant from very early on ($<1\% = <0.5$ cm of y -movement, see gray significance bar in Fig. 2) until the end of the reach (100% = 40 cm of y -movement). Follow-up functional comparisons (2-level repeated measures) confirmed that there was one distinct trajectory toward each of the single targets (cyan and dark-red significance bars), and another toward the middle of the display when two potential targets were presented. The trajectories on two-target trials did not differ until much later in the reach (pink significance bar, Fig. 2).

Having demonstrated a replication of the spatial averaging we had observed earlier, we then tested how these midpoint trajectories were affected by consecutively cueing the same target position. In Fig. 3 we present the trajectory results for trials that were con-

secutively cued left (Fig. 3A) or right (Fig. 3B). Each line represents averaged reaching behaviour for the different number of target repetitions to one side. It is readily apparent from the figure that acting on a cued target on one side of space biases one toward that side on the next trial and that this effect is cumulative. That is, the initial trajectory between the two targets is increasingly pulled toward the side that is repeatedly cued as the number of consecutive trials to that side increases. This was confirmed statistically by analyzing all possible functional pair-wise comparisons between the five levels of sequence (1–5). With ten comparisons per cued-side it was convenient to represent the significance bars of these comparisons in matrix form (see Fig. 3C). Each row and column (counted outward from the middle) corresponds to a different number of consecutively cued trials (colour-coded by row to match the trajectories). Each row–column intersection shows the significance levels over time for the functional comparison between those two trajectories (with spatial and significance coding being a condensed form of the bars in Fig. 2). This pattern of reaches being biased toward the side of space that was consecutively cued was also evident when we analyzed behaviour on the Switch trials (see Supplemental Figure 1), the pattern of Miss errors (see Supplemental Figures 2 and 3) and the temporal kinematics (see Supplemental Table 1). Another pattern that emerged in all of these analyses was that the bias created by trial repetitions to the right developed and saturated more quickly than the bias created with repetitions to the left. For instance, we see differences emerging when comparing reaches on the first and second of consecutive trials, but only on the right side (see top row of Fig. 3C). We also see that differences do not persist as strongly when comparing reaches for a higher number of repetitions to the right but are still present even between reaches on the fourth and fifth repetition to the left (bottom row, Fig. 3C).

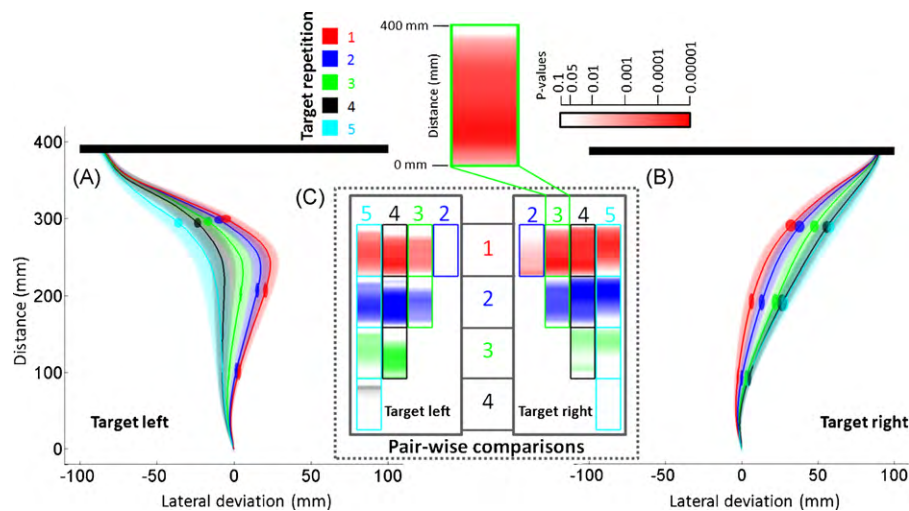


Fig. 3. Averaged three-dimensional reach trajectories from all Repetition trials in repeat-left (A) and repeat-right (B) micro-sequences shown from the above view with formatting as in Fig. 2. Each coloured trajectory represents reaching behaviour at a different position in the repeat sequence: (1) red, (2) blue, (3) green, (4) black, and (5) cyan. (C) Functional pair-wise comparisons between all possible pairs of trajectories (separated left and right) arranged as a matrix. Each row and column corresponds to a different position in the repeat-sequence with the intersection being the comparison between those two trajectories. Within each intersection box, the position of the coloured area corresponds to the locations along the reach distance (y) where the trajectories differed in the lateral (x) dimension, with the intensity of the colour corresponding to the magnitude of the statistical difference (see exploded box at the top).

4. Discussion

Effective goal-directed behaviour in a dynamic environment requires a nervous system that is able to flexibly adapt its current behaviour based on prior experience. The ease with which the visuomotor system incorporates previous events into current motor plans demonstrates just how sophisticated and highly adaptable the underlying decision processes are [29]. Indeed, as we show here, earlier experience with particular targets can affect the weightings assigned to those and other targets competing for action selection: acting on a target on one trial biased participants toward that same target position on the next trial. In other words, by measuring reach trajectories made toward displays with two potential targets, we showed that subjects initiate a spatially averaged trajectory that is cumulatively biased in the direction of previously cued targets. This provides clear evidence that one of the factors affecting competition between simultaneously encoded motor plans is trial history.

One theory explaining the effects of trial history on reaching argues that the parameters defining an action are not reset each movement but built by modifying the parameters of the preceding movements [27]. This carryover of motor parameters can explain why, in our study and others, an accumulation of the trial history effect is observed. For example, Whitwell and Goodale [21] showed that grip apertures became wider when visual feedback was consecutively unavailable (or smaller when it was consecutively available) and that the magnitude of these effects grew across four repeated trials. Similarly, where Maljkovich and Nakayama [19] showed a reaction time benefit to detect a target at a repeated location, they were able to attain a significant advantage for repetitions up to five trials later. These previous findings are highly consistent with our results showing that spatial biases in reach trajectories, as induced by consecutive target cueing, accumulate over the course of 4–5 trials.

Interestingly, in contrast to the Maljkovich and Nakayama finding [19] and other studies demonstrating that repeating some task-relevant target feature (e.g. colour, shape, location) yields faster reaction times [7,19,22,30], we found that reaction time was not affected by consecutive cueing (see Supplemental Table 1). While this was somewhat unexpected, we believe this reflects differences in the task demands. For example, in the Maljkovich

and Nakayama study [19] a visual search task was used with free-varying reaction times of ~ 600 ms, while in the current study a strict reaction time cut-off of 325 ms was employed (resulting in average reaction times of < 250 ms). This reaction time demand almost certainly superseded any sequence effects that may have been present, and is consistent with null reaction time effects we have seen previously using a similar paradigm [6].

As several measures we analyzed reveal, the way in which these spatial biases accumulate differs slightly depending on the side of space that the consecutively cued target is presented. Specifically, participants seem to have some baseline bias toward the rightward target, and as such, the bias developed by consecutive cueing in that direction developed more quickly and saturated with fewer repetitions than consecutive cueing to the left. The underlying reason for this baseline preference for rightward targets is likely biomechanical in nature (all participants made reaches with their dominant right hand), an effect that has been reported previously [6,31]. It will be interesting for future experiments to examine the number of consecutive trials over which these effects can accumulate. Specifically, when do these effects begin to saturate and how is this affected by the intertrial interval?

Our findings that reach trajectories are initially aimed at a midpoint between potential targets is consistent with theories suggesting multiple motor plans are activated in parallel and averaged when actions are executed [1,10,32]. By using initial trajectories as a spatial correlate of a competition between potential targets, we show in the current experiment how trial history influences this competition with initial movements biased toward the location of the previously cued target position. The source of these biases may come from the effects of repeated cueing on the 'attentional landscape'. Recently, it has been persuasively argued that the context and demands of goal-directed grasping and reaching tasks directly influence the distribution of attentional resources across the workspace (referred to as an attentional landscape, for review see [33]). This division of attention into multiple spatial foci can be probed by requiring participants to detect transient changes in stimuli that can occur at either grasp/reach-relevant or -irrelevant locations immediately prior to the movement. It is typically found that participants can reliably detect these stimuli changes in locations where the hand must move (e.g. near stable object grasp points for both the thumb and finger) but when these

stimuli changes occur elsewhere (e.g. locations unrelated to the upcoming movement), participants perform at chance. In the current experiment, attentional resources might initially be equally allocated to both potential targets locations, but with consecutive cueing of one of these locations, the attentional landscape could shift to provide more processing resources for that location, resulting in additional trajectory shifts toward that target. We suspect that the shifting landscape and the resulting short-term motor plasticity are a direct result of biases in neural decision processes in the brain areas involved in reach planning and execution (e.g. parietal and premotor cortices [34–36]). Indeed, neurons in dorsal premotor (PMd) cortex have been shown to simultaneously encode multiple potential reach directions prior to the decision to make one of the movements [5] and the preparatory neural activity in eye-movement structures (i.e. superior colliculus, frontal eye-fields) is also strongly influenced by trial history [14,22,23].

In conclusion, our rapid reach paradigm provides a unique visualization of how visuomotor decision-making processes evolve not just within a single movement, but also over the course of multiple movements. In particular, our use of novel functional data analysis techniques [28] allowed us to precisely quantify how the action undertaken on a previous trial can influence future motor decisions. This revealed subtle trial-to-trial effects which would go largely unnoticed by the conventional approach of averaging across multiple trials/movements [e.g. [14]]. Moreover, our task and analysis extend previous methodologies and show that visuomotor decision-making processes can be measured in a continuous fashion through time-evolving reach trajectories rather than the discrete measurements (e.g. response times) used in typical tasks (e.g. key presses, verbal reports). In contrast with other previous measures (e.g. % of correct responses), our task also shows that target encoding is not even tied to the final choice made by the participant: initial trajectories are influenced only by the probability of acting at each target location and recent trial history (number of repetition trials) and not by the target location that is cued in-flight during the movement.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found in the online version, at doi:10.1016/j.bbr.2010.05.012.

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