

Visual salience dominates early visuomotor competition in reaching behavior

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In this study, we investigated whether visual salience influences the competition between potential targets during reach planning. Participants initiated rapid pointing movements toward multiple potential targets, with the final target being cued only after the reach was initiated. We manipulated visual salience by varying the luminance of potential targets. Across two separate experiments, we demonstrate that initial reach trajectories are directed toward more salient targets, even when there are twice as many targets (and therefore twice the likelihood of the final target appearing) on the opposite side of space. We also show that this salience bias is time-dependent, as evidenced by the return of spatially averaged reach trajectories when participants were given an additional 500-ms preview of the target display prior to the cue to move. This study shows both when and to what extent task-irrelevant luminance differences affect the planning of reaches to multiple potential targets.

Keywords: motor planning, reaching, visual salience, attention, perception, action, luminance

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Introduction

Goal-directed movements are typically performed within a complex, target-rich visual milieu. How does the

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human visuomotor system select from among so many competing targets and distractors? One possibility is that the visuomotor system constructs maps that encode the behavioral priority of the respective stimuli in the visual scene (Bisley & Goldberg, 2010; Fecteau & Munoz, 2006).

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In these priority maps, cells facilitate activity in other cells with similar processing preferences and inhibit activity in cells with different preferences. The net result is a landscape of competing neural populations, each representing a potential target for attention and/or action (Baldauf & Deubel, 2010; Cisek & Kalaska, 2005; Desimone & Duncan, 1995). Some have argued that the activity within priority maps not only represents the behavioral priority of stimuli but also constitutes an ongoing elaboration of parallel motor plans for interacting with the respective stimuli (Cisek, 2007).

While the majority of evidence for the parallel encoding of multiple motor plans has come from monkey electrophysiology (Baldauf, Cui, & Andersen, 2008; Basso & Wurtz, 1997; Cisek & Kalaska, 2005; McPeck, Han, & Keller, 2003), support can also be found in a large body of behavioral work. For example, when a target and a distractor are positioned in close proximity, eye movements tend to initially deviate toward the distractor, resulting in a curved trajectory (Godijn & Theeuwes, 2002; Sailer, Eggert, Ditterich, & Straube, 2002; Theeuwes, Kramer, Hahn, & Irwin, 1998; Van der Stigchel, Meeter, & Theeuwes, 2006). Similarly, in reaching behavior, this “spatial averaging” has been observed between target and distractor (Sailer et al., 2002; Song & Nakayama, 2008) and in response to probabilistic information about eventual target location (Hudson, Maloney, & Landy, 2007). Models of saccade generation explain this spatial averaging effect as the result of unresolved competition between possible targets in the priority map (McPeck et al., 2003; Port & Wurtz, 2003).

In a series of recent studies, we set out to test a specific behavioral prediction arising from competition-based models of the spatial averaging effect; we predicted that if participants were forced to reach toward multiple potential targets, the unresolved competition between the potential targets would result in a spatial averaging of reach trajectories. In these studies, participants initiated rapid reaches toward multiple potential targets, all of which had an equal likelihood of being cued as the final target upon movement initiation. At movement onset, the final target was cued and participants corrected their reach trajectory in flight to the cued location. Initial trajectories resembled a spatial average of individual trajectories toward all potential targets, reflecting biases from both the spatial location and number of potential targets on each side of space (Chapman et al., 2010a, 2010b; Gallivan et al., 2011). If, as we will argue, this paradigm allows researchers to get a real-time glimpse of an unresolved competition between *individual targets* represented in the priority map, then it could prove to be a useful, non-invasive technique for investigating the mechanisms of visuomotor decision-making in humans.

Note that the pattern of results described in the multiple target reaching (MTR) paradigm described above is

consistent with any explanation based on the simultaneous encoding of multiple targets (and/or movement plans) within visuomotor planning networks. In other words, it leaves untouched the question of whether or not this type of processing is occurring in something like a priority map. Given that priority maps incorporate both cognitive and stimulus-driven inputs (Desimone & Duncan, 1995; Trappenberg, Dorris, Munoz, & Klein, 2001) and are especially modulated by stimulus salience (Findlay & Walker, 1999; Koch & Ullman, 1985), one should predict that the introduction of task-irrelevant luminance differences into an array of potential targets would result in the spatial averaging of reach trajectories being modulated and biased toward the high luminance targets. Indeed, there is evidence that the spatial averaging of saccades can be influenced by luminance differences (Deubel, Wolf, & Hauske, 1984), but, to our knowledge, no one has investigated how task-irrelevant luminance differences in multiple potential targets affect the planning of a reach to those targets. Thus, the present study utilizes the MTR paradigm to investigate the question of how the representation of visual salience in the priority map influences the evolution of competition between multiple potential targets for action.

To fully address the question of how salience influences the unfolding of visuomotor competition, it was necessary to probe the state of that competition at more than one time point. This temporal aspect of the experimental design was also motivated by the finding that salience seems to exert only a transient effect upon visual selection (Theeuwes, 2010). For example, when reporting the location of the most salient singleton in a display, participants were most accurate at short response latencies and short presentation durations (Donk & van Zoest, 2008). In another study, when participants were asked to indicate the location of a probe, reaction times (RTs) were significantly faster when that location was previously occupied by a salient singleton than when it was occupied by a background stimulus. Importantly, this effect was observed only when the singleton display was presented for relatively short durations (e.g., 30–240 ms); by 480 ms, there was no RT difference (Dombrowe, Olivers, & Donk, 2010). Together, these studies suggest that there is an early and brief temporal window within which visual salience biases the competition for selection.

For the present study, therefore, we predicted that salience would overpower the spatial averaging effect when presentation durations were short but that there would be no effect of salience (as evidenced by the return of spatial averaging) when presentation durations were relatively long. To test this, we manipulated the timing of the task such that some participants were required to begin their reaches immediately upon presentation of the potential targets, while others were required to wait 500 ms before being cued to begin their reach. Our results

suggest that visual salience exerts a time-dependent bias upon the competition between multiple potential movement plans.

Experiment 1

Methods

Using OPTOTRAK (NDI, Waterloo), we recorded rapid reach movements (sampling the position of the right index finger at 150 Hz) in 22 right-handed subjects as they reached from a start button to a touch screen located 40 cm away (Figure 1A). Trials began with participants holding down the start button while fixating a cross at the center of the screen (for 1000–2000 ms). A beep signaled that the fixation cross had been replaced by a target display that consisted of one or two potential targets [hollow circles (2-cm diameter) of black pixels on a white background]. This beep also served as a cue for subjects to initiate a reach toward the display (within 325 ms). It is important to note that fixation was no longer required after the target display replaced the fixation cross. Upon button release, one of the targets in the initial display was cued (by filling in black) and subjects had to modify their trajectory in flight to that target location within 425 ms (Figure 1B). All targets in the display had an equal probability of filling in and becoming the final target. To encourage accurate performance, participants received trial-by-trial feedback on their fulfillment of the task's temporal and spatial constraints. There were four possible types of errors that caused the following text to be displayed: *Too Early* (if the start button was released before 100 ms had elapsed after the beep; this aborted the trial), *Time Out* (if the start button was not released within 325 ms; this also aborted the trial), *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. The timing constraints used in the present study have been used in past studies that employed a version of this task (Chapman et al., 2010a, 2010b; Gallivan et al., 2011). Participants performed an initial training session of at least 32 trials, followed by 160 test trials (across 10 blocks).

We manipulated the visual salience of the targets by varying the number of pixels contributing to the targets themselves (Figure 1C). High-salience targets consisted of hollow, black circles (i.e., the line of the circle consisted of 100% black pixels). For the low-salience targets (which were the same size as the high-salience targets), we randomly replaced half of the black pixels of the circle with white pixels (the same color as the background), thus yielding a stimulus with exactly half the contrast of the high-salience target. The initial target display only ever consisted of one or two targets, with the two possible

target locations being in the same vertical plane and equidistant from the location of the central fixation cross and separated by 18 cm.

Prior to statistical analysis, we removed trials with the slowest 5% of movement times (between subjects) as well as trials where participants missed the target. In order to be included in the final analysis, participants had to contribute at least four successful repetitions of each trial type across the experiment. After trial removal, 6 participants failed to meet this criterion and were excluded from analysis, leaving 16 of the original 22 participants for inclusion in the statistical analysis.

Results

We used repeated-measures functional ANOVAs (FANOVAs) to compare spatially normalized (in the Y dimension) trajectories across conditions of interest (Ramsay & Silverman, 2005). This technique allows one to examine both where and to what extent trajectories are statistically different within a given dimension (here, we used deviation in the X dimension). See our previous work (Chapman et al., 2010a, 2010b; Gallivan et al., 2011) for a more detailed description of this analysis technique.

Initial trajectories showed a significant bias toward the higher salience target (Figure 2). When high-salience targets were presented on the left, trajectories were biased toward the left side of space (green traces in Figure 2). Similarly, when high-salience targets were presented on the right, trajectories were biased toward the right side of space (blue traces in Figure 2). Importantly, this was the case whether the final target was cued on the left or the right (Supplementary Figure 1). In contrast, when equally salient targets were presented on both the left and right sides of space (i.e., when both targets were either high or low salience), subjects showed no such biasing and initial trajectories aimed for a midpoint between the two targets (red and black traces in Figure 2). The FANOVA showed that trajectories toward targets of unequal salience (i.e., L:H and H:L) were significantly different from trajectories toward equally salient targets (i.e., L:L). These differences started early (2.5% of the reach) and continued until near the end of the reach (94% of the reach).

Experiment 2

There were at least three potentially relevant consequences of varying the concentration of pixels in the targets of Experiment 1 (E1): First, the targets varied in number of pixels. Second, they varied in the luminance contrast of their contours (i.e., the luminance of the background vs. the luminance of the lines making up the target). Third, they varied in the overall luminance contrast of the target (i.e., the luminance of the background

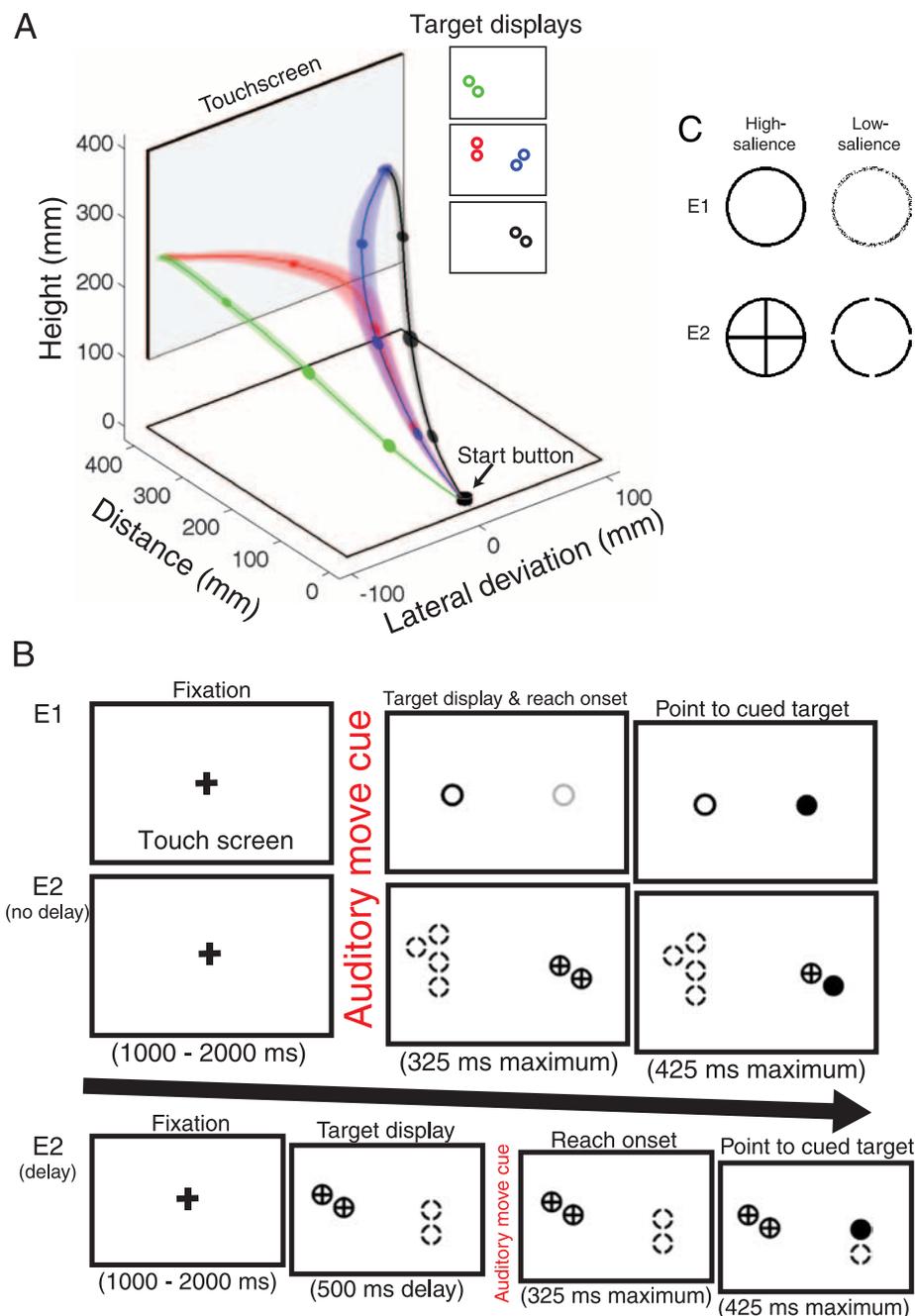


Figure 1. Illustration of (A) the experimental setup and typical arm trajectories, (B) the tasks, and (C) the experimental stimuli. The three-dimensional view of the experimental setup (A) depicts reach trajectories for sample target displays, averaged across 27 participants. The color of the trajectory corresponds to the initial target displays (inset right) and, in the case where potential targets appeared on both sides of space (i.e., blue and red targets), the final target location. The shaded bands surrounding the trajectories represent average standard error. The size of the three darkened ovals is proportional to velocity in the X and Y dimensions at 25%, 50%, and 75% of movement distance. Colors are for purposes of illustration only. (B) Following the presentation of a fixation cross for a random interval, potential targets were displayed on the left and/or right sides of a touch screen. In E1 and the E2 no-delay group, the appearance of the potential targets was accompanied by an auditory cue for the participants to release a start button and initiate reach with the index finger toward the target display within 325 ms. In the E2 delay group, the auditory cue to move came 500 ms after the initial target display had appeared. In every case, the appearance of the final target (indicated by one of the potential targets filling in black) was triggered by the release of the start button as participants initiated their reaches. Participants had to touch the final target within 425 ms after button release. As displayed in (C), targets in [Experiment 1](#) (E1: top row) consisted of black circles with contours of either 100% (high salience) or 50% (low salience) pixel concentration. In [Experiment 2](#) (E2), the high-salience target consisted of a black circle overlaid with a black cross, while the low-salience target consisted of a black circle with pixels removed where a cross would have intersected with the circle.

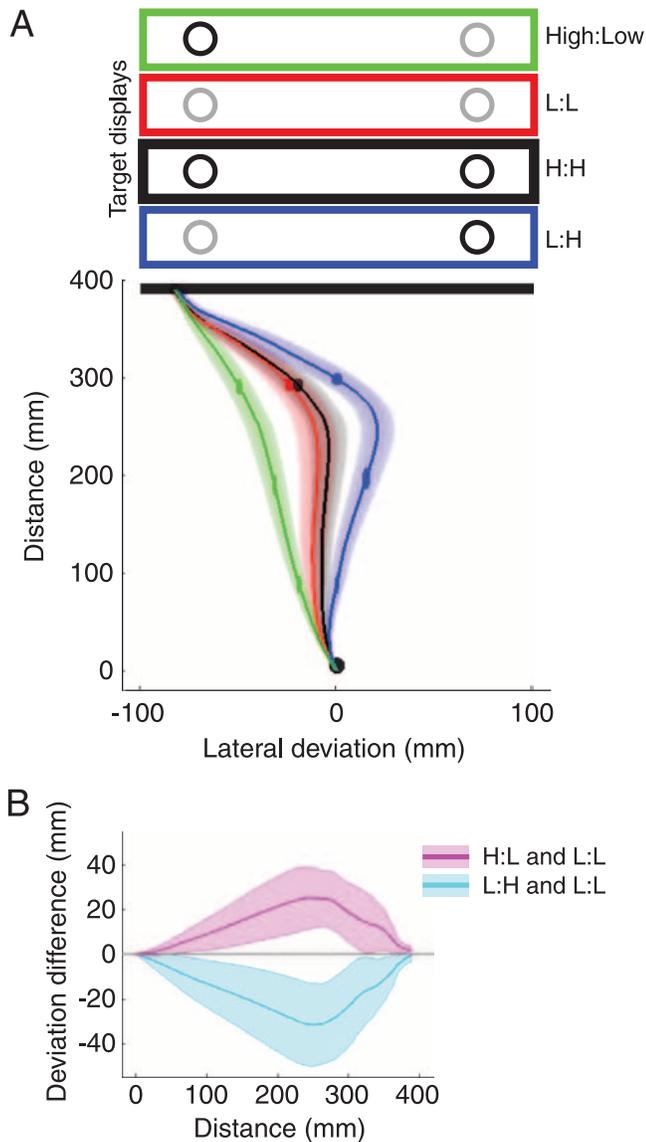


Figure 2. Results from [Experiment 1](#): (A) An overhead view of average reach trajectories toward the target displays was indicated above the plot. Only trials in which the left target was cued are shown. Shaded areas in the trajectory plot represent average standard error. The dark lines in (B) indicate the lateral deviation difference between trajectories in the H:L [i.e., *high*-saliency target (left side of target display) versus *low*-saliency target (right side of target display)] and L:L conditions (magenta) and between trajectories in the L:H and L:L conditions (cyan). Shaded areas in the difference plot represent 95% confidence intervals.

vs. luminance within the bounds of the target). Any of these factors could conceivably be responsible for the biasing of initial trajectories toward the high-saliency targets in E1.

The second experiment (E2) had three goals: first, to disentangle the influences of number of pixels and contour luminance contrast from that of target luminance contrast;

second, to observe how saliency interacts with the number of potential targets in the biasing of initial reach trajectories; and third, to see whether the saliency bias (if there is one) is constant within the time scale of a single trial or whether it changes as a function of time.

To address the first goal of E2, we took a basic target (i.e., empty black circle) and either subtracted (low saliency) or added (high saliency) a cross at its center, with the arms of the cross spanning the diameter of the circle (see [Figure 1C](#)). The two resulting stimuli had equal contour luminance contrast, but they differed in target luminance contrast and the low-saliency stimulus still had half as many pixels as the high-saliency stimulus. Our interest in the question of pixel count was primarily motivated by a need to rule out the possibility that, in past versions of our task ([Chapman et al., 2010a, 2010b](#)), trajectory biases toward the side of space with more targets could be attributed to the fact that the side with more targets also always had more black pixels on a white background. In other words, rather than basing reach decisions on the probabilities inherent in the spatial distribution of targets, participants could have simply used differences in the amount of “stuff” on each side as a cue for initial trajectory formation. In theory, when presented with twice as many low-saliency targets on one side as there are high-saliency targets on the other side, participants could: (1) be pulled toward one side because of high-saliency targets, (2) be pulled toward the other side because of a greater number of targets (and thus a greater probability that the final target would appear on that side), or (3) not be pulled to either side and reach up the middle because there would be an equal number of pixels on each side of space.

Accordingly, we addressed the second goal of E2 by varying the number of potential targets that could appear on each side of the screen ([Figure 1B](#)). Either 0, 2, or 4 targets could appear on each side of the screen (i.e., all permutations of 0:2, 0:4, 2:2, 2:4, and 4:4 across the two levels of the saliency factor). Target locations were selected from a hexagonal cluster of possible locations (with one location at the center, resulting in 7 possible target locations) on each side of the screen, with the center target of the cluster being located 9 cm to the left or right of the central fixation cross ([Supplementary Figure 2](#)). The addition of more targets necessitated more trials to ensure a suitable number of trial-type repetitions. After an initial training session of at least 54 trials, an experimental session commenced, consisting of 540 trials (10 blocks of 54).

To address the third goal of E2, we tested two separate groups of participants. Participants in one group (no-delay group) were presented with the initial target display at the same time that they received an auditory cue to begin their reach. The other participants (delay group) received the auditory cue 500 ms after the presentation of the initial target display ([Figure 1B](#)). This time-dependent approach allowed us to investigate what effect, if any, target saliency might have when subjects have been given more time to process the target display and plan their reaches.

We have emphasized that the targets employed in E2 differed in overall target luminance (i.e., luminance within the bounds of the target) but not in contour luminance (i.e., luminance of the lines that make up the target). We note here that another possible factor introduced by this salience manipulation is the relative closure of the target contours. The high-salience target had fully closed contours, while the low-salience target had open contours. In light of evidence that shape processing is fast for closed stimuli and slow for open stimuli (Elder & Zucker, 1993), we assumed that the degree of closure of the E2 targets also contributed to their overall salience.

Methods

Aside from the differences mentioned above, the design and procedure of E2 were identical to those of E1. There were 31 participants in the no-delay group and 33 participants in the delay group. After trial removal and

participant screening (using the same criteria that were used in E1), we were left with 27 participants in the no-delay group and 26 participants in the delay group.

Results

The primary finding of E2 was that salience differences (i.e., global luminance contrast) strongly biased the trajectories of participants in the no-delay group. This bias was strong enough to overpower the traditional spatial averaging (based on the distribution of targets) that we have observed in earlier studies (Chapman et al., 2010a, 2010b; Gallivan et al., 2011). In contrast and rather importantly, we found no salience bias in the trajectories of participants in the delay group. Instead, their trajectories showed a return to spatial averaging behavior (Figure 3).

This time-dependent effect of salience can be observed in the comparison of 2H:2L (i.e., two *high*-salience targets on the left versus two *low*-salience targets on the right)

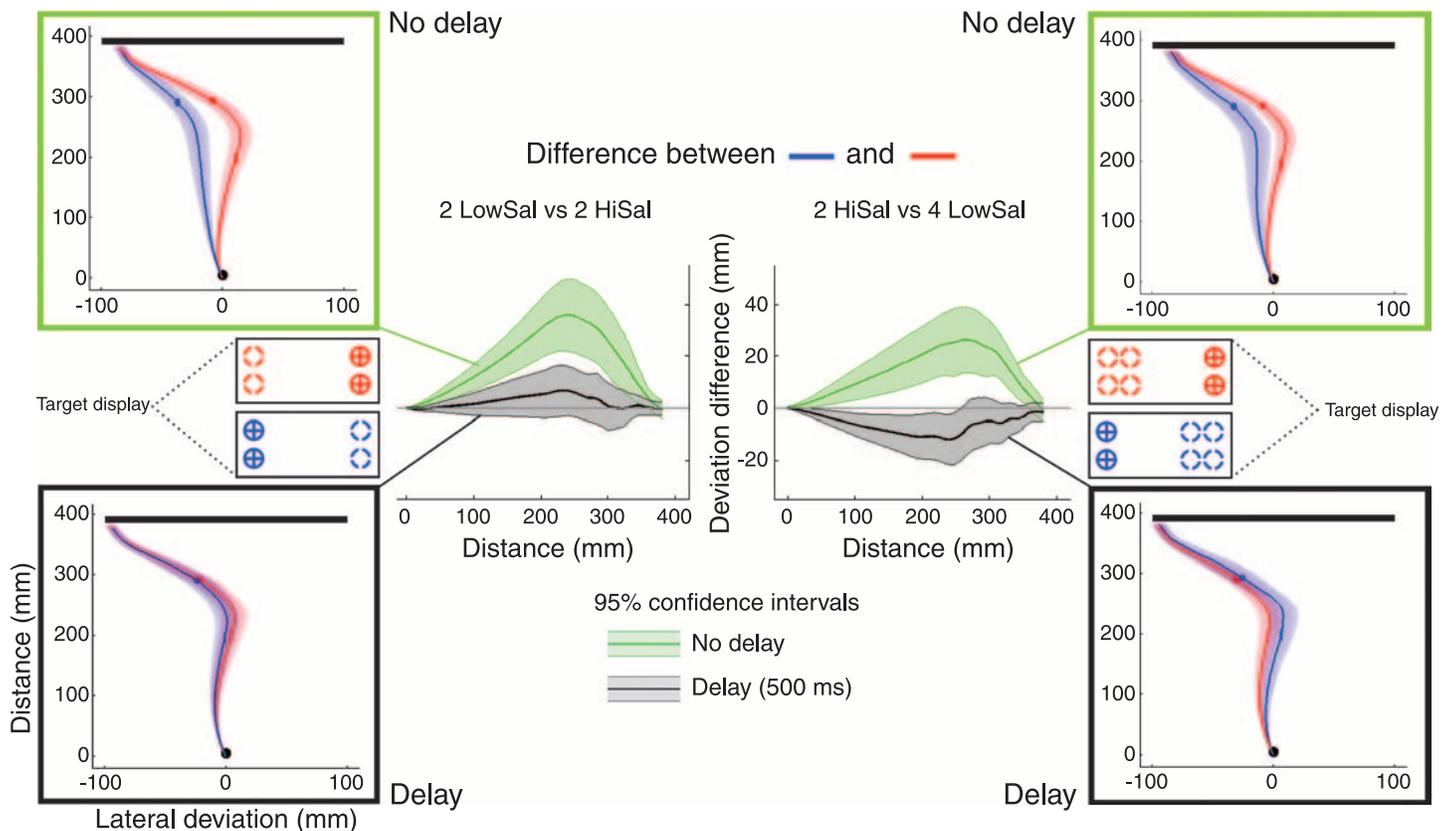


Figure 3. Results from Experiment 2. The two plots on the left show an overhead view of average trajectories for the no-delay (top plot) and delay (bottom plot) groups in response to a target display with two low-salience and two high-salience targets. The color of the trajectories correspond to the color-coded target displays depicted between the two plots. In these plots, and in all other plots in the figure, only trials where the final target appeared on the left are shown. The two plots on the far right show average trajectories of the no-delay (top plot) and delay (bottom plot) groups in response to four low-salience and two high-salience targets. Shaded areas in the trajectory plots (i.e., blue and red) represent average standard error. Colors are for purposes of illustration only. The two plots in the center of the figure show the difference in lateral deviation (between the red and blue trajectories; i.e., the difference between responses to the two spatial arrangements of a given target display) as a function of the distance between the hand and the touch screen. Shaded areas in the difference plots represent 95% confidence intervals.

and 2L:2H trials. Initial trajectories were biased toward the side with the high-salience targets in the no-delay group. In the delay group, however, both of these trajectories ran up the middle, as would be predicted if participants in the delay group were simply averaging the spatial location of the potential targets.

A more striking illustration of this effect of salience came from the comparison of 4L:2H and 2H:4L trials. Even though the final target was twice as likely to appear on the side of space with the four low-salience targets, initial trajectories of participants in the no-delay group were still strongly biased toward the two high-salience targets. Critically, in the delay group, we observed a small but significant bias toward the side of space with more potential targets.

We observed an unexpected attenuation of spatial averaging sensitivity in the no-delay group, even in trials where all potential targets had equal salience. For example, when we compared 2H:4H and 4H:2H trials, the FANOVA showed that trajectories were only slightly biased to the left when there were four targets on the left and only slightly biased to the right when there were four targets on the right (Supplementary Figure 3). Regardless of this attenuation, spatial probabilities still had a consistent effect on reaches such that trajectories were always biased toward the side of space with more targets.

As an alternative to the results of the functional data analysis presented here, we also performed a more traditional analysis of the same data, using a mixed-design ANOVA that compared averages of a selected data point (i.e., 30% of the reach trajectory) instead of the entire reach trajectory. This analysis was entirely consistent with the functional data analysis and is included in the Supplementary materials (see Supplementary Table 1). An analysis of reaction time (Supplementary Table 2) and movement time (Supplementary Table 3) for E2 is also included in the Supplementary materials.

General discussion

We recorded trajectories while subjects performed reaches toward multiple potential targets of differing luminance. Two basic observations emerged: (1) when subjects were required to react immediately, trajectories were strongly biased toward the side of space containing targets of higher salience, even when a higher number of less-salient targets on the opposite side of space made this strategy suboptimal, and (2) when subjects were given a 500-ms preview of the initial display of potential targets prior to being cued to move, the salience bias was profoundly diminished, as evidenced by the return of a spatial averaging trajectory bias that reflected the target probabilities inherent in the initial display. These results, to our knowledge, are the first to show that target salience exerts

a time-dependent modulation of the spatial averaging of reach trajectories.

Salient targets dominate early visuomotor competition

The driving motivation behind the present study was to test the hypothesis that the neural mechanisms responsible for selecting a reach target would be influenced by luminance differences in the potential targets. More specifically, we hypothesized that the competition between representations of potential targets on a reach-specific priority map would be biased by salience differences such that the neural activity representing salient target(s) would be facilitated. In light of our claim that the spatial averaging effects observed in past iterations of the present task (Chapman et al., 2010a, 2010b; Gallivan et al., 2011) and other similar tasks (Hudson et al., 2007; Song & Nakayama, 2006, 2007, 2008) are a reflection of unresolved competition in the priority map at the time of reach initiation, one clear prediction from this hypothesis was that the unresolved competition would be biased in favor of the salient target(s), resulting in an initial trajectory bias toward the spatial location of the salient target(s). This prediction was also based on an analogy with models of saccade curvature (McPeck et al., 2003; Tipper, Howard, & Houghton, 2000; for a review, see Van der Stigchel et al., 2006), in which saccade curvature during double-step (Van Gisbergen, Van Opstal, & Roebroek, 1987) or visual search paradigms (Godijn & Theeuwes, 2002; McPeck, Skavenski, & Nakayama, 2000; Walker, McSorley, & Haggard, 2006) is a result of averaging disparate saccade vectors encoded simultaneously by competing clusters of activity within a priority map.

In the present study, when participants were required to initiate a reach as quickly as possible (E1 and no-delay group in E2), initial trajectories were strongly biased toward the high-salience targets. This is in contrast to spatially averaged trajectories that aim for a midpoint location when the salience of the competing targets was equal. A more compelling demonstration of this salience bias (in E2) was found in the observation that when making rapidly initiated reaches, trajectories were biased toward high-salience targets even when there were twice as many targets (and therefore twice the probability that the final target would appear) and an equal number of pixels on the other side of space. The fact that trajectories did not aim for a midpoint location in this condition (i.e., 2H:4L) suggests that the salience bias is driven not by the difference in salience between whole clusters of targets (i.e., the amount of pixels or “stuff” on a given side of space) but rather by the difference in salience between individual targets.

One surprising observation from E2 was that when salience was held constant (e.g., 2H:4H), initial trajectories were far less sensitive to spatial target probabilities

than has been observed in past studies (Chapman et al., 2010a, 2010b; Gallivan et al., 2011). Perhaps the introduction of luminance differences, along with the overwhelming behavioral relevance of visual salience in most other contexts, cultivated a readiness for those differences even though they were task-irrelevant in this case. On a related note, the observed behavior of participants in the no-delay group during the 2H:4L condition also shows that the salience bias exerts dominance not only in spite of the task-irrelevance of target luminance but also in spite of a considerable decrease in movement efficiency. In other words, reaching toward the 2H targets (as opposed to the 4L targets) in response to the 2H:4L display necessitated a greater frequency and magnitude of online corrections. This seemingly suboptimal behavior persisted throughout the entire session (i.e., there was no detectable difference between behavior in the first three and last three blocks; see [Supplementary Figure 4](#)), suggesting that participants in the no-delay group never learned to ignore the salience of targets.

At least one study has previously examined the role of target salience in the selection of reaching movements. Zehetleitner, Hegenloh, and Müller (2011) observed that when participants pointed to a target among a uniform field of distractors differing from the target in either orientation or luminance, reach durations and initiation latencies decreased as feature contrast increased. Since a similar effect has been consistently observed in saccades during visual search tasks (cf. Wolfe & Horowitz, 2004), Zehetleitner et al. interpreted their results as evidence of a salience map. In the present study, we were unable to detect differences in initiation latencies between trials with and without luminance differences between targets. Indeed, we have never been able to detect reaction time differences in past implementations of the present paradigm—a fact that is likely a reflection of the stringent reaction time cutoff employed (i.e., 325 ms). Importantly, the failure to detect RT differences was not due to participants “timing out” more often on one type of trial than another, which would have led to a selective exclusion of the more difficult trials from analysis. Simply put, participants quickly learned to respond well ahead of the cutoff (the slowest average RT for any condition was 200 ms; see [Supplementary Table 2](#)), regardless of luminance conditions. Despite the lack of RT differences, the results of our trajectory analysis agree with the claim that reaching movements are selected on the basis of a motor map that incorporates visual salience into its computations.

Multiple studies indicate that there is typically a tight anchoring of ocular gaze to the target of ongoing pointing movements (Fisk & Goodale, 1985; Neggers & Bekkering, 2000). Indeed, it could be argued that eye movements are often an integral component of visually guided reaching; we typically look at the target we are reaching for. Given that eye movements were unconstrained in our study, one might argue that the observed effect of salience upon initial reach trajectories could be explained by salience-induced saccadic

activity prior to the initiation of the reach. That is, salient targets could have captured attention and elicited a saccade, and pointing movements could have been drawn to where the participants were looking. We acknowledge this possibility and hope to pursue this interesting question in future studies.

Visual salience is a factor only during early visuomotor competition

One of the central goals of the present study was to test the prediction that if salience did in fact bias initial reach trajectories, it would do so only within a short temporal window after the presentation of the potential targets. Positive support for this prediction was found in the striking reversal of trajectory biases as participants in the no-delay group were biased by target salience while, within the same condition, participants in the delay group were instead biased by the spatial distribution of potential targets (see [Figure 3](#)). These results agree with a number of studies showing that eye and arm movements following either a short SOA or a short response latency are more influenced by salience differences than are those that follow longer SOAs or response latencies (Dombrowe et al., 2010; Donk & Soesman, 2010; Donk & van Zoest, 2008; Stritzke, Trommershäuser, & Gegenfurtner, 2009). The results of the present study and these latter studies indicate that target salience biases selection only within a brief time span following stimulus onset.

Why does the salience bias seem to disappear after a few hundred milliseconds? One possible explanation is that stimulus salience results in an immediate and persistent boost in gain at the corresponding location on the priority map and that the gain at this location can be suppressed by top-down inputs that take a few hundred milliseconds to appear. More specifically, some have proposed that the initial sweep of activity during visual processing is entirely stimulus-driven and that subsequent recurrent processing involves top-down regulation of early visual areas by way of long-range feedback connections (Lamme & Roelfsema, 2000; Theeuwes, 2010). This proposition finds some empirical support from a study in which Buschman and Miller (2007) recorded simultaneously from frontal (prefrontal cortex and frontal eye fields) and parietal (lateral intraparietal area, LIP) cortex while monkeys located a target in either a visual popout or a visual search task. These two tasks were meant to selectively elicit bottom-up or top-down attention, respectively. Interestingly, LIP cells represented the location of the target 150–200 ms earlier in the popout task than they did in the visual search task, suggesting that bottom-up attention has an influence upon the priority map in LIP significantly sooner than does top-down attention.

Of course, in everyday behavior, visual information is not broken into the discrete, unpredictable bursts that characterize visual information within a laboratory setting.

Rather, visual information tends to be continuous, contextualized, and statistically structured, which implies that anticipatory top-down modulation could occur in principle, allowing one to suppress task-irrelevant salience differences within a stimulus set. Indeed, Mazaheri, Diquattro, Bengson, and Geng (2011) have demonstrated that pre-stimulus coupling between frontal and parietal areas predicted successful suppression of attentional capture by a salient distractor. Many other studies have demonstrated that it is possible to suppress attentional capture from the outset, specifically when sufficient practice or training has occurred (Ipata, Gee, Gottlieb, Bisley, & Goldberg, 2006; Kim & Cave, 1999) or when task set (Yantis & Egeth, 1999) or distractor frequency (Geyer, Müller, & Krummenacher, 2008) increases the incentive to suppress salience differences (although the results of Yantis and Egeth have been strongly contested; see Lamy & Zoraris, 2009). It is conceivable that, in our task, participants could have eventually developed the ability to suppress the salience bias had they been given more trials.

An alternative explanation of the eventual disappearance of salience biases is that salient stimuli are processed earlier than other competing stimuli, as indicated by electrophysiological studies (Hickey, McDonald, & Theeuwes, 2006; Töllner, Zehetleitner, Gramann, & Müller, 2011). In priority maps, where lateral inhibition results in winner-take-all dynamics (Bisley & Goldberg, 2010), a selective reduction in processing latency for salient stimuli would also result in the suppression of activity at other spatial locations prior to the appearance of activity representing less salient stimuli. After the appearance of the other stimuli, and in the absence of any continuous signal boost for salient stimuli, the competition would tend toward equalization until either endogenous or exogenous inputs identified and thus biased the competition for one of the targets. This “head start” is another possible mechanism that could explain the time dependence of the salience bias in our data.

Conclusion

In conclusion, we show that salience exerts a time-dependent bias upon reach trajectories toward multiple potential targets and that this salience bias overpowers the spatial averaging of initial trajectories toward those targets. Since this spatial averaging behavior is widely thought to reflect unresolved competition in a priority map, we interpret our results as evidence that visual salience selectively increases the gain of target representations on the map and that this early processing advantage for salient targets dwindles within 500 ms at most. It will be important for future studies to titrate the duration of the display presentation (prior to the movement cue) in order to better characterize the shape of the function describing the attenuation of the salience bias.

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