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RESEARCH ARTICLE

Eye movements are primed toward the center of multiple stimuli even when the interstimulus distances are too large to generate saccade averaging

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Abstract Prior oculomotor research has established that saccades tend to land near the center of multiple saccade targets when they are near each other. This saccade averaging phenomenon (or global effect) has been ascribed to short-distance lateral excitation between neurons in the superior colliculus. Further, at greater inter-stimulus distances, eye movements tend toward the individual elements. This transition to control by local elements (individuation) with inter-stimulus distance has been attributed to long-range lateral inhibition between neurons in winner-take-all models of oculomotor behavior. We hypothesized that the traditional method of requiring a saccade to an array of multiple, simultaneous targets may entail response ambiguity that intensifies with distance. We resolved the ambiguity by focussing on reaction time of our human participants to a single saccade target after one or more simultaneous priming stimuli. At a 50-ms prime-target interval, saccadic reaction time was shortest for targets closer to the center of the prime stimuli independent of the distance between the primes. This effect was gone at 400 ms. These findings challenge the typical inferences about the neural control of oculomotor behavior that have been derived from the boundary between saccade averaging and individuation and provide a new method to explore eye movements with lessened impact from decision processes.

Keywords Priming · Eye movement · Global effect · Local effect · Saccade averaging

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Introduction

Coren and Hoenig (1972) and later Findlay (1982) discovered that saccadic eye movements tend toward the geometric midpoint of simultaneously presented and spatially proximal visual stimuli. This finding that the aggregate stimuli bias saccade landing position toward the spatial midpoint is referred to as saccade averaging (or the global effect). Ottes et al. (1984) replicated this finding but noted further that, as visual stimuli are placed further apart, the saccade tends to land at one of the possible visual targets, a finding we refer to as saccadic target individuation (a local effect). The boundary between averaging and individuation (or between control by the global stimulus array versus its local elements) has been well documented (Findlay 1997; Chou et al. 1999; Findlay and Brown 2006; Van der Stigchel et al. 2011; Van der Stigchel and Nijboer 2013). Many now accept that saccadic averaging is most robust when visual stimuli are separated by less than 20–30° of angular distance (Walker et al. 1997) so long as the visual stimuli appear beyond the foveal dead zone (i.e., a 1°–1.5° of visual angle radius at fixation) and within the region of behaviorally relevant stimuli (see Vitu 2008, for review).

Saccadic averaging and individuation are typically precipitated by the presentation of multiple simultaneous visual stimuli. The effect of such stimuli on oculomotor systems, especially the superior colliculus (SC), has been studied at the neural level in the rhesus monkey (e.g., Edelman and Keller 1998; Glimcher and Sparks 1993; Van Opstal and Van Gisbergen 1990; Dorris et al. 2007), and at the behavioral level in both monkeys (e.g., Chou et al. 1999) and humans (e.g., Van der Stigchel et al. 2012). Findings from such investigations have informed computationally explicit and neurophysiologically plausible models of oculomotor responding (Wilimzig et al. 2006; Satel et al.

2011; Wang et al. 2012a, b). These models account for the transition between averaging and individuation responses by assuming short-distance excitatory and long-distance inhibitory connections between neurons in the SC (Van Opstal and Van Gisbergen 1989). The short-distance excitation causes input-elicited activation from spatially proximal visual stimuli to fuse together, driving the saccadic landing site toward the midpoint, hence the saccadic averaging. The long-distance inhibition allows for distal inputs to inhibit one another, permitting saccade selection between one of the stimulated sites in a winner-take-all fashion, hence saccadic individuation. Despite the popularity of the preceding account of the boundary between saccade averaging and individuation, the notion of long-distance inhibitory connections remains controversial (Arai and Keller 2005; Isa and Hall 2009; Lee and Hall 2006; see Marino et al. 2011 for a summary of the debate).

We believe that the transition to saccadic individuation in the saccade averaging paradigm is probably not originating at the level of the SC, and that the mistaken attribution that it does originate there is a contributing factor to this controversy. As suggested by Kowler (1990), the standard behavioral approach to evaluating the boundary between averaging and individuation runs the risk of conflating higher-level cognitive (e.g., decision-level) processes with lower-level oculomotor events (see also Van der Stigchel et al. 2011, for some consideration of this matter). The traditional method of presenting two targets simultaneously, with the consequent ambiguity in instructions (e.g., "select one," or "move to the stimuli"), ensures that the saccade landing site will reflect a combination of involuntary input-elicited oculomotor response activation and adaptations to comply with task demands.

Precisely because of these foregoing concerns, we eschew the traditional method in favor of a priming method requiring no saccade selection mechanisms at the time of multiple, simultaneously appearing visual stimuli. The method we propose is based on a long history of priming research that explores the automatic activation of pathways by stimuli that are not predictive about the upcoming stimulus or correct response. In the current study, multiple, to-be-ignored visual stimuli (a prime array) appear simultaneously, followed immediately by a single saccade target (see Fig. 1) so as to ensure that no decisions regarding saccade metrics are required at the time of the prime. To determine the effect of these visual stimuli on the oculomotor processing dynamics, we evaluate how saccadic response latency to a single response probe is influenced by its relative distance to the Euclidean midpoint of the priming array.

The historically inclined reader will notice that our methodological recommendation for the world of oculomotor pathway activation is analogous to the much earlier innovation recommended by Posner and Snyder (1975) for the world of semantic pathway activation. Using a task with multiple targets (letter strings), Meyer and Schwaneveldt (1971) discovered that participants were faster to report that two targets were both words when the letter strings were related words than when they were the unrelated. To overcome interpretive ambiguities associated with this interesting finding, Posner and Snyder recommended replacing the dual-target task with one that explored the effect of a word prime upon the processing of a single, subsequent, word target, a recommendation that launched the fecund semantic priming paradigm (cf Neely 1976, 1977). As such, the critical dependent variable will be saccadic reaction time (SRT), which we assume will reflect the activation state of the oculomotor system at the time of the target (e.g., saccades toward locations activated by the prime array will be facilitated relative to other, non-activated locations).

Given the somewhat dramatic departure from prior saccade averaging studies, which emphasize measurement of various saccade metrics, we realize that researchers who study the consequences of multiple visual targets on

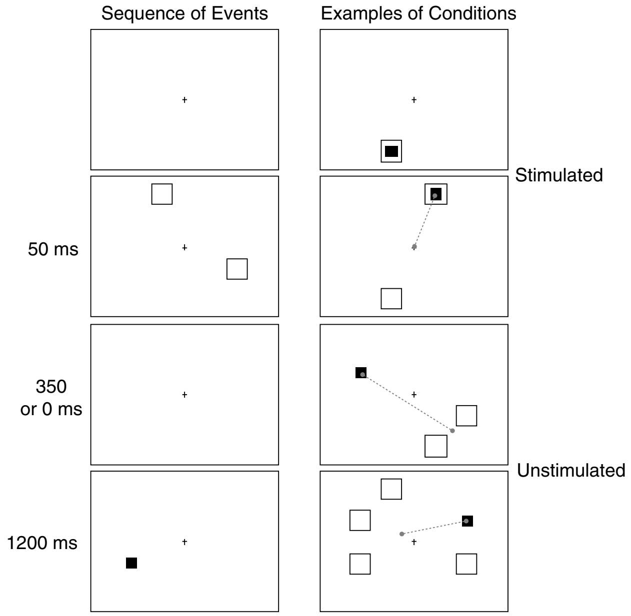

Fig. 1 Sample displays of the experiment, with contrast reversal for readability. The left sequence of panels depicts a typical trial. There could be 1, 2, or 4 prime stimuli in any of 8 locations located 8.5° from fixation. The target could appear in either a previously stimulated or unstimulated location. In the depicted example, there are two primes and an unstimulated target location. The right 4 panels show some sample conditions. The primes and targets did not appear simultaneously as depicted in the examples, but are shown this way for illustrative purposes. The *gray dashed lines* and *dots* were not presented to participants but depict the distance (*lines*) between the center of the primes (*dots*) and the target. Example previously stimulated target locations are illustrated in the *top* two panels following 1, and 2 primes. Previously unstimulated target locations are illustrated in the *bottom* two panels following 2 and 4 element primes

oculomotor processing may nevertheless be anticipating results about errors or deviations in saccadic responding with respect to target position. We stress that saccade metrics are not the focus here. Firstly, the design of the study precludes a straightforward interpretation of the metrics with regards to the center of the primes versus individual prime stimuli. Indeed, because of the traditional method of requiring saccadic eye movements to one of the multiple visual targets invoking higher-level decision-making processes, we turn to a priming method requiring no response decision at the time of multiple visual stimuli. Secondly, single targets are presented alone and at an unpredictable location; as such, one would not expect previous priming stimuli to influence saccade landing positions (Wang et al. 2012b; Watanabe 2001).[1]

Further incentive for the proposed method has arisen from recent work, investigating whether the phenomenon inhibition of return (IOR; Posner et al. 1985; Klein 2000) is generated at the center of multiple to-be-ignored stimuli or the locations of individual stimuli (Christie et al. 2014; Klein et al. 2005; Langley et al. 2011). It is well known that oculomotor IOR—operationally defined by delayed ("inhibited") responding at the location(s) of prior exogenous orienting responses some time (>~200 ms) after the orienting stimulus—is generated by the primitive midbrain structures responsible for reflexively generated saccades (Hilchey et al. 2014; Posner et al. 1985), specifically the SC (Godijn and Theeuwes 2002; Sapir et al. 1999; Sereno et al. 2006). Even non-primate species lacking fully developed cortical structures and whose visual orienting depends principally on the optic tectum exhibit IOR (Gabay et al. 2012), a finding that lends further credence to the notion that IOR is generated via subcortical oculomotor structures. Given that both saccadic averaging and oculomotor IOR are commonly thought to be represented by the internal processing dynamics of low-level oculomotor response systems, one should expect that IOR and saccadic averaging would share a boundary between averaging and individuation. Contrary to this expectation, IOR data were best accounted for by the center of the stimulus array, unbound by inter-stimulus distance (Klein et al. 2005; Christie et al. 2014).

Accepting that IOR is the inhibition of orienting toward the location(s) of exogenously generated oculomotor response program(s), we reasoned that we would likewise be able to observe evidence of a facilitatory aftereffect of an array of stimuli (a prime) at its center of gravity regardless of the distance between stimuli in the priming array at short (<100 ms) onset asynchronies between the prime and target. If the prior behavioral work on saccade averaging is correct about the averaging and individuation boundary, then the saccade toward the target should be influenced by the center of the prime array when the prime array stimuli are close to each other but by the individual items when interstimulus distances are large. If SC responses inferred from IOR studies are correct, then the center of the prime array should prime eye movements regardless of interstimulus distance and act as the primary determinant of reaction time to a subsequent target.

Finally, we note that although our focus is at a short PTOA, we included a longer prime to target stimulus interval (prime to target onset asynchrony or PTOA), similar to that used in IOR studies. While this longer PTOA may appear favorable for generating IOR, we departed from the method pioneered by Klein et al. (2005) by omitting the cue-back to fixation (e.g., Pratt and Fischer 2002) between the prime and target. Our preliminary testing without this methodological feature suggested that influences of the center of stimuli would not appear at this PTOA, presumably because the observer does not reliably disengage from the primed location (e.g., MacPherson et al. 2003). Thus, we expected little to no behavioral effect of priming at the center of gravity at the late PTOA despite small albeit consistent effects of the individual stimuli. This late interval is included in our experiment primarily to validate the sensitivity of our analytical approach for discriminating aggregate and individual effects of the stimuli.

Methods

Participants

Fifteen University students with normal vision volunteered to participate in this experiment and were compensated with either one point of course credit or $10 Canadian. Two were excluded from analysis exceeding a 25 % anticipation criterion. The research was conducted with the approval of the relevant Dalhousie Research Ethics Board.

Apparatus and stimuli

Participants were tested in a dimly lit room with stimuli presented on a 19″ ViewSonic Optiquest Q95-3 CRT monitor at a 58-cm viewing distance connected to an Apple Mac

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[1] Results from trials with single primes and nearby (45° away) targets allowed us to confirm the null results reported with single targets from the studies by Wang et al. (2012a, b) and Watanabe (2001). Saccade landing positions were measured with respect to how much they deviated toward or away from that primeQuery. At the 50 ms PTOA the mean of deviation was 0.17° (away from the cued side), 95 % CI = [−0.09°, 0.42°]. At the 400 ms PTOA the mean deviation was −0.3° (toward the cued side), 95 % CI = [−0.6°, 0.01°]. Thus, in agreement with Wang et al. and Watanabe, with confidence intervals that include zero, there is no compelling evidence here to suggest that single primes bias saccade landing sites when single targets are presented at unknown locations.

Mini Core Duo. An EyeLink II eye monitor tracked eye movements from the initiation of a drift correction until the end of the trial. After participants performed a 9-point calibration procedure, the Eyelink sampled gaze position once every 4 ms.

All stimuli were presented in white against a black background. The fixation stimulus was a central cross-measuring 0.5 × 0.5° of visual angle. The primes were unfilled squares measuring 2°× 2° with a border 2 pixels thick. The target was a filled square measuring 1 × 1° degree. The prime and target stimuli appeared at one of the eight equally spaced positions along the circumference of an imaginary circle with a radius of 8.5°, as illustrated in Fig. 1. There were 750 trials/participant selected at random with replacement.

Procedure

Trial sequences and schematics of stimulus layout are presented in Fig. 1. Each trial started with the central fixation, which was always present, and a manual spacebar response made by the participant when they were ready. The events of the trial unfolded at this point if the eye monitor detected relatively stable fixation. Otherwise, a beep was sounded and the participant would press the space bar again when ready. This drift corrected the eye monitor and, when stable fixation was achieved, a 1, 2, or 4 prime element array immediately appeared for 50 ms with each element in a randomly selected location. Participants were informed that these primes were irrelevant to the task, should be ignored, and to maintain fixation. Either immediately after the offset of the prime (50 ms prime-target stimulus onset asynchrony—PTOA), or after a 350-ms interval (400 ms PTOA), the target appeared and participants made a saccade toward it. The target appeared onscreen for 1200 ms. Participants could take a break at any point during the experiment by refraining from initiating a trial. See Fig. 1 for examples of stimuli and depiction of the trial sequence.

Data preparation

There were several steps in data preparation before analyzing the SRT. Eye movements that started within 20 ms of target onset were immediately discarded as impossibly fast (blinks were not differentiated from other kinds of eye movements here). Eye movements were recorded as correct if the angle of the initial trajectory fell within 12.5° on either side of the target's direction, yielding 97.2 % correct movements overall. Given a skewed and sparse long tail on the SRT distribution, and many fast SRTs, an assessment of the SRT distribution was undertaken using 10 ms bins to determine upper and lower SRT cutoffs that were based on trends in accuracy. It was found that acceptable accuracy was not reached until 130 ms at the 50 ms PTOA and 90 ms at the 400 ms PTOA, with 50 % or poorer performance at shorter times. Consequently, all SRTs shorter than those cutoffs were believed to be anticipations and removed from further analysis. Long SRTs were also examined, and it was found that, given a decline in accuracy and the diminishing amount of data as SRT increased, about 610 and 440 ms for the 50 and 400 ms PTOAs, respectively, were judicious cutoffs for believing that the SRT was not a response to the onset of the stimulus but perhaps a response to the recognition of the presence of the stimulus at a later time. This trimming based on distribution and accuracy removed 5.1 % of the trials, the majority of which were anticipations, with only 0.5 % of the total being longer than 450 ms. The accuracy of the remaining trials was so high, 99.5 % on average with many conditions 100 %, that an analysis of accuracy was not possible.[2] The SRT analyses are based on the correct remaining trials.

When the resulting distribution was assessed with Box-Cox (Box and Cox 1964) transformations, it was discovered that the distribution of the inverse of SRT (1/SRT) approximated a normal distribution better than the untransformed SRTs. As a consequence, analyses were performed on −1/SRT. Residuals of the models were also checked for normality, and because the variability between participants is so much greater than the effects in the data, the initial transformations on raw data were deemed satisfactory. Nevertheless, for the purpose of portraying the results, the data were back-transformed to SRTs in milliseconds, where this could be done reasonably. It is useful to note that, while we did back-transform the data, the only justification is convention. The inverted score can simply be interpreted as the number of eye movements that could be made/second, or rate. It is presented as negative rate so that increasing values are more easily interpreted by those expecting SRTs.

The analysis was conducted using the lme4 package (Bates et al. 2014) in R (R Development Core Team 2011) using linear mixed effects regression. The analysis is reported primarily like regression results with "b" indicating the slope of the predicted line. This is a linear mixed modeling approach that does not have an agreed upon degrees of freedom for statistical tests of the fixed effects. We chose bootstrapped confidence intervals to report both an estimate of effects and to allow people to infer their own test results if they wish.

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[2] Further examination of errors in landing position revealed that the median Euclidean distance between landing position and the center of the target for the correct trials was approximately 1°. There was also no relationship between accuracy of landing position and SRT ($r = -0.03$).

Results

See the methods for detailed information on data preparation. Analyses were based on correct SRTs. In order to normalize residuals, inverse SRTs, or rates, were modeled (-1/SRT in seconds), but for the purpose of displaying the results, the data were back-transformed to SRTs where reasonable, (e.g., figures), but not where it was inappropriate, [e.g., regression coefficients (b)].

It was first established, due to warning signal effects, that there was a large effect of time between prime and target onset (or prime-target onset asynchrony, PTOA). SRTs were 81.9 ms shorter at the long PTOA 95 % CI = [80.5, 83.2]. Moreover, PTOA interacted with all other factors of interest. The results from the two PTOAs are so obviously different, as seen in Fig. 2 and highlighted in Table 1 where no effect CIs overlap across PTOA, that the two PTOA conditions were analyzed separately.

At the 50 ms PTOA, there is approximately a 23 ms disadvantage, 95 % CI = [18.5, 29.6], for previously stimulated (285 ms) versus unstimulated (262 ms) target locations from these trials (which is apparent in the difference in height between the green and blue data in the left panel of Fig. 2).

Regression coefficients for the analyses can be seen in Table 1. All of the 50-ms PTOA prime conditions have increasing SRTs as targets are moved away from the geometric center of the prime array. At the later PTOA, the slope is reversed and shallower. For the single prime element condition, the slope of the line was calculated, leaving the one stimulated target location out because of the large effect of stimulation.

Additional analyses were performed on the trials for which targets did not appear at a location where there had been a prime element because, with these trials, the effect of distance between the target and the nearest prime element can also be analyzed. We compared models using AIC (Akaike 1974; Symonds and Moussalli 2011) because this method, which is asymptotically equivalent to cross-validation, allows the necessary comparison of non-nested models (i.e., center of prime model and nearest prime model are not nested but also not orthogonal). When the 50-ms PTOA condition was analyzed, a model containing both the distance to nearest prime element and distance to center of the elements yielded an effect of the center, $b = 44.3 \times 10^{-3}$, $\mathrm{SE} = 8.54 \times 10^{-3}$, 95 % CI = $[27.4 \times 10^{-3}, 61.8 \times 10^{-3}]$, but not of the nearest stimulus, $b = -10.0 \times 10^{-3}$, $\mathrm{SE} = 7.80 \times 10^{-3}$, 95 % CI = $[-25.6 \times 10^{-3}, 5.8 \times 10^{-3}]$.

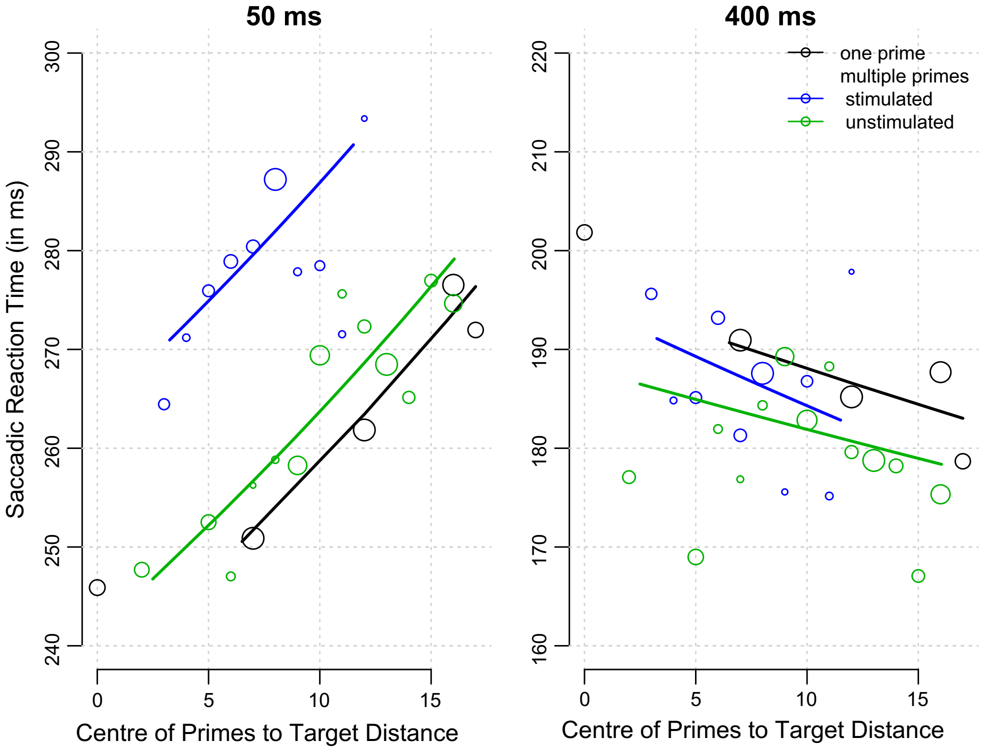

Fig. 2 SRT as a function of the distance between the center of the prime array and the location of the target in degrees of visual angle. The size of each circle is proportional to the number of trials within that condition. Data plotted in *black* are from trials with a single element prime. The *green* and *blue* data come from trials with multiple element primes. *Green* represents data from trials for which the target was presented at a previously unstimulated location, while *blue* is for trials in which the target location was previously stimulated (color figure online)

Table 1 The significand of regression coefficients, standard errors, and confidence intervals that went into calculating the lines in Fig. 2 in scientific notation

Prime	PTOA (ms)	*b*	SE	95 % CI
Single element	50	37.0	5.05	27.9, 47.0
	400	−27.0	5.64	−37.5, −16.3
Target at a prime stimulus location	50	31.7	10.00	10.2, 50.0
	400	−30.3	16.17	−64.2, 3.0
Target at a new location	50	36.2	5.57	24.1, 47.4
	400	−19.4	8.87	−36.8, −0.7

The multiplier for all is 10^{-3} . These values are all in the analyzed scale (−1/SRT in sec or negative rate). In order to make the figures in msec, they were back-transformed after calculating final points. See text for a discussion of the cause of these effects

Assessment using AIC revealed that the center of the prime model alone was the best with AIC 26 lower than for nearest element predictor alone and 20 lower than with both predictors included. The conclusion is that distance to the nearest prime element has almost no unique explanatory power for SRTs over and above its correlation with the center of the primes. In contrast, when the same analytic strategy was applied to the 400 ms PTOA condition, it was revealed that the negative trend found when the center of the prime elements was the predictor was due to the correlation with the distance to the nearest prime element. At this PTOA, distance to nearest prime element is the best model with AIC 8 lower than the center of primes only model and 12 lower than a model containing both. When both are entered together, the effect of center of the prime elements is positive, $b = 10.2 \times 10^{-3}$, SE $= 13.22 \times 10^{-3}$, 95 % CI $= [-15.6 \times 10^{-3}, 37.4 \times 10^{-3}]$, while the unique effect of the nearest stimulus is stronger and negative, $b = -37.2 \times 10^{-3}$, SE $= 12.33 \times 10^{-3}$, 95 % CI $= [-63.4 \times 10^{-3}, -13.5 \times 10^{-3}]$. Therefore, the negative slopes observed in Fig. 2 at the 400 ms PTOA are due to the nearest prime stimulus and not the aggregate prime array.

In order to determine whether increasing the spacing of the elements in the multiple prime arrays reduced the influence of the center of the elements, the data from unstimulated multi-element prime targets at the 50 ms PTOA were analyzed by dividing trials into those with relatively compact versus distributed prime element arrays. This was done by making a median split on the distance of the prime array center from fixation. Maximally distributed arrays will have the prime center at fixation, while maximally compact ones will have the prime center at the most peripheral locations. In the condition where two prime stimuli are immediately adjacent, the correlation between distance to nearest prime stimulus and distance to center of the prime array is 0.99 so that condition had to be excluded. Figure 3 illustrates the effect of distance from the target to the center of gravity of the prime array for both compact, $b = 29.5 \times 10^{-3}$, SE $= 9.44 \times 10^{-3}$, 95 % CI $= [11.4 \times 10^{-3}, 48.0 \times 10^{-3}]$, and distributed prime arrays, $b = 67.0 \times 10^{-3}$, SE $= 12.31 \times 10^{-3}$, 95 % CI $= [42.0 \times 10^{-3}, 89.9 \times 10^{-3}]$. Clearly, the primes with relatively distributed elements are generating saccadic averaging that is not weaker than that generated with more compactly distributed prime elements. A model of the primes with distributed elements including only distance to the center of the primes had an AIC 28 lower than for a model containing only distance to nearest prime. A model including both predictors was not as good as the model with the center of primes predictor alone (ΔAIC = 1). This finding is in stark contrast to that expected from prior studies that found eye movements made to simultaneous targets that were far apart generated evidence for target individuation.

Discussion

With all stimuli presented on the circumference of an imaginary circle centered on fixation, our participants made saccades to a single target (filled square) that was preceded by a spatially uninformative array of prime stimuli (larger, unfilled squares). The prime array consisted of 1, 2 or 4 elements. The degree to which the prime array activated the oculomotor system was inferred from SRTs to the target, with faster SRTs implying greater activation. Our focus was upon the relative contribution of the prime array's global and local properties to this activation function. At the shortest interval between the prime array and saccade target, oculomotor responding was fastest near the geometric midpoint of the array, independent of prime array inter-stimulus distance.

This novel SRT finding challenges the conclusions which have been drawn from extant behavioral and neurophysiological studies that established boundaries between saccadic averaging and saccadic individuation depending on inter-stimulus and/or angular distance (e.g., Van der Stigchel et al. 2011). Effects of the center of the stimuli on SRT are ubiquitous at all inter-stimulus distances so long as no ambiguous decision about where to direct a saccade is required at the time that the array of multiple stimuli is presented. In contrast, to our findings with multiple prime stimuli and single targets, studies with multiple targets present observers with an ambiguous task. We propose that this ambiguity elicits task-induced adaptations that originate outside the SC. As such, dynamic neural field models that reproduce stimulus individuation for spatially distant visual targets are probably mistaken in attributing this boundary entirely to computations within the SC.

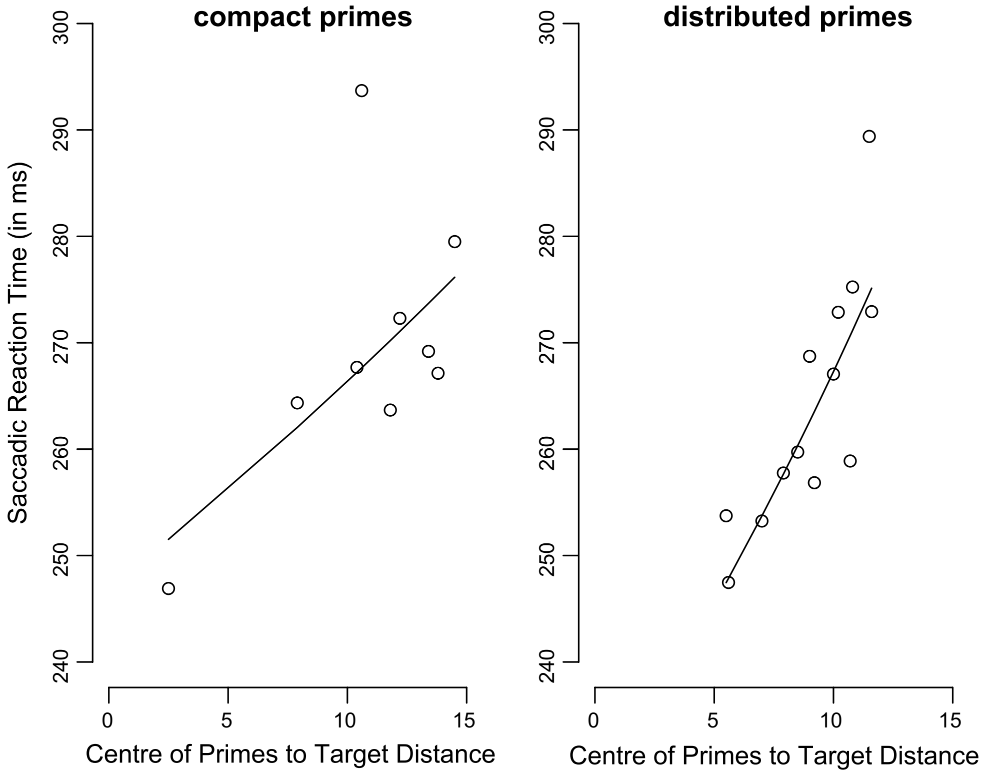

Fig. 3 The multiple prime unstimulated target 50-ms PTOA condition (*green* data in *left* panel of Fig. 2) separated into trials with compact and distributed prime arrays. Because 4 element prime arrays are included, the compactness of the array is measured by the distance of the center of the prime array from fixation. A maximally distributed prime array would have the center at fixation, while a very compact one would be close to the periphery where stimuli appear. The dividing point for compact and distributed prime arrays was a distance of the center of the array from fixation of 3.4°

Further evidence for this proposal can be found in a classic study by Robinson (1972, see also Schiller et al. 1979) in which, among other things, saccade averaging was explored in response to microstimulation across a broad range of SC sites. For our purposes, the critical finding was that electrical stimulation of two SC sites invariably resulted in averaging saccades, even at angular distances typically conducive to stimulus individuation with multiple targets. While this paper is widely cited, this particular finding has been largely ignored by oculomotor theorists, perhaps in part because its results conflict with the dual-target findings from behavioral studies. However, as in the priming method used here, the approach using electrically evoked saccades avoids the confounding consequences of instructing the observer to choose one among multiple saccade targets. Providing converging evidence for our proposal, SRTs are longer under conditions producing stimulus individuation than those that elicit saccadic averaging (Ottes et al. 1984; Van der Stigchel et al. 2011; Walker et al. 1997). In lieu of the conventional explanation positing an effect of long-distance inhibition, our proposal attributes the delayed responding to a high-level decision process that is invoked by a bias to select one among multiple visual stimuli for responding that gets stronger as items are farther from each other.

At the longer interval between the prime array and saccade target, the aggregate effect of the prime array was replaced by weaker, inhibitory effects of the individual elements. Therefore, our new effects of aggregate stimuli were not merely a side effect of this particular analysis because it is also sensitive to gradients around individual stimuli. We note that the cost at stimulated relative to unstimulated locations, most notably at the shorter prime to target interval, does not generate a gradient around those stimuli. In fact, the small gradient effects of the nearest stimulus at the shorter interval were generally positive.

In conclusion, when multiple targets are presented simultaneously, there is a boundary between averaging and individuation that has been observed at short and long interstimulus distances, respectively. The present findings, with multiple prime stimuli and single targets, challenge, not this boundary, but rather its use in modeling the organization of oculomotor behavior at the level of the SC. Through our methodological improvements (presenting a single target minimizes the influence from higher-level decision processes upon saccade programming), we have shown that averaging of oculomotor activation occurs robustly over much greater interstimulus distances than previously imagined. This finding undermines any model of saccadic behavior that seeks to explain the boundary between global and local control that is observed with multiple targets entirely in terms of the neural organization of the SC. This challenge applies whether the boundary is implemented through the relative contributions of short-range excitatory and long-range inhibitory connections or through some other means at the level of the

SC. We propose that the boundary between control by the global stimulus array that gives rise to saccade averaging and control by the array's local elements that produces saccadic individuation in multiple target paradigms is more aptly accounted for by high-level decision-making processes invoked when a choice is required among multiple visual stimuli than by the internal processing dynamics of low-level oculomotor response systems (see Meeter et al. 2010 for a similar suggestion for the remote distractor effect). When the contribution from such high-level decision processes is removed from the response, the most activated region of the saccade map is at the center of gravity of an array of stimulus elements regardless of inter-stimulus distance.

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Conflict of interest None.

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