Parametric integration of visual form across saccades

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ABSTRACT

Through saccadic eye movements, the retinal projection of an extrafoveally glimpsed object can be brought into foveal vision quickly. We investigated what influence visual detail collected before the saccade exerts on the postsaccadic percept. Participants were instructed to saccade towards a peripheral stimulus, and to indicate on a continuum of ellipses with varying aspect ratios which exact shape they had perceived to be present after saccade landing. Compared to both an identical ellipse preview and a qualitatively different square preview, a quantitatively different ellipse preview was observed to shift the mean postsaccadic percept towards the presaccadic aspect ratio parameter value. This integration of subtly different form information was accompanied by an integration of the identity of both stimuli presented: In the great majority of these trials, subjects indicated that they had not noticed the occurrence of a change to the stimulus. When a blank screen preceded the postsaccadic stimulus onset the influence of presaccadic stimulus information on postsaccadic perception was weaker. An immediate postsaccadic mask on the other hand abolished the effect entirely. We conclude that integration of parametric visual form information occurs across saccades, but that it relies on a quickly decaying and maskable visual memory.

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1. Introduction

Outside the fovea, the quality of the visual input delivered by the human retina to the brain is severely degraded. This limited spatial extent of high-acuity vision compels the observer to frequently perform saccadic eye movements in order to extract relevant visual detail from the surrounding scene. Consequently, at least two sources of information are available on each object to which a saccade is directed: Peripheral or parafoveal information collected before the saccade, on the basis of which the visual system decided to foveate this object next, and foveal information obtained during the subsequent fixation. The question then arises exactly which presaccadic information – if any – is stored in transsaccadic visual memory until saccade landing, and in what way this information could be employed to facilitate postsaccadic visual processing of the same object.

McConkie and Rayner (1976) initially suggested that perceptual evidence collected across fixations accumulates in a spatiotopic integrative visual buffer, underlying transsaccadic fusion of even low-level visual information. Despite the appealing simplicity of this idea, little empirical evidence could be found to support it. Whereas spatiotopic fusion would predict presaccadic and postsaccadic experimental displays to appear as being overlaid on top

of one another, subjects failed to explicitly combine simple patterns across saccades, and proved to be highly inaccurate at detecting intrasaccadic changes to stimulus position or form (Bridgeman, Hendry, & Stark, 1975; Bridgeman & Mayer, 1983; Grimes, 1996; Jonides, Irwin, & Yantis, 1983; Li & Matin, 1990; O'Regan & Lévy-Schoen, 1983; Rayner & Pollatsek, 1983; Verfaillie, 1997). Implicit improvements of postsaccadic recognition performance following a relevant presaccadic preview could be observed, but only to the extent that they shared coarse structural information; similarity in visual detail or precise metrical stimulus properties did generally not result in facilitative effects (Carlson-Radvansky & Irwin, 1995; Henderson, 1997; Henderson, Pollatsek, & Rayner, 1987; Irwin, Zacks, & Brown, 1990; Pollatsek, Rayner, & Collins, 1984; Pollatsek, Rayner, & Henderson, 1990; Rayner, McConkie, & Zola, 1980). As a result, it was suggested that transsaccadic object representations only contain relatively coarse, abstracted information on the presaccadic display. Irwin and colleagues (Irwin, 1991, 1992; Irwin & Andrews, 1996; see also Prime, Tsotsos, Keith, & Crawford, 2007) specifically showed that transsaccadic visual memory shares many properties with regular visual short-term memory (VSTM), in that the abstracted information it contains is long-lasting and non-maskable, but limited in capacity to about four distinct items. Indeed, VSTM's strong focus on encoding categorical or relational information could then be what severely impedes the discrimination, explicit combination, or postsaccadic facilitation by presaccadic preview of fine visual detail across a saccade.

Deubel, Schneider, and Bridgeman (1996, 2002), however, demonstrated that at least the failure to detect stimulus changes coinciding with a saccade is not to be attributed to a lack of precise encoding of stimulus position or form information into transsaccadic visual memory. In their studies, transsaccadic discrimination accuracy improved greatly when the display was blanked briefly during and immediately after the saccadic eye movement, before the onset of the postsaccadic stimulus. This suggests that a transsaccadic representation of considerable precision is present into the next fixation, that can however not be explicitly compared to newly incoming postsaccadic stimulation unless a postsaccadic blank interval is introduced. Similarly, we have shown in a recent study (Demeyer, De Graef, Wagemans, & Verfaillie, 2009) that a presaccadic preview of detailed visual form information can still affect postsaccadic object identification performance, but only under the specific experimental condition of a sufficiently high postsaccadic perceptual uncertainty. That is, presaccadically obtained visual detail can only be observed to be actively employed in postsaccadic visual processing when the observer stands to gain enough from using this information in addition to the currently present visual input. Specifically, we presented subjects with highly similar, meaningless closed form contours at low contrast and short exposure durations, and observed that identical presaccadic preview stimuli improved postsaccadic identification accuracy, compared to no-preview conditions. A non-identical but still highly similar preview resulted in even worse identification accuracy than the no-preview baseline measurement. However, these preview effects disappeared when an immediate postsaccadic mask interrupted stimulus presentation. We proposed that a detailed but visually maskable memory trace underlies these results, on the basis of which presaccadic and postsaccadic information on the saccade target object form can be integrated. When the presaccadic preview stimulus is identical to the postsaccadic target stimulus, the reliability of postsaccadic perception increases, reducing random errors during identification. A non-identical but highly similar preview object, on the other hand, would then bias the integrated form percept towards the presaccadic object form estimate, inducing systematic identification errors.

The aim of the present study is to validate these claims with more direct empirical evidence. To this end, we would like to distinguish between two possible interpretations of the concept of transsaccadic integration in visual object recognition.

Informational integration is the phenomenon where the postsaccadic object form percept is influenced by the object form contents of the presaccadic display. Given a shared metrical stimulus space in which both the stimuli themselves and the resulting percept(s) can be located, the benefit of an identical preview could be seen as a reduction in the spread of postsaccadic percepts around the veridical postsaccadic stimulus value. Qualitatively different, uninformative previews that cannot be located within the same metrical space will result in a veridical mean, but with a larger spread than is the case in identical preview conditions, owing to the uncertainty that is a property of the isolated postsaccadic stimulus information, as well as to potential forward masking. Non-identical previews that can still be expressed as a value within the same metrical space, on the other hand, would then mainly shift the mean of the distribution of postsaccadic percepts to an intermediate position between the pre- and postsaccadic stimulus values. Two specific alternate explanations for the postsaccadic identification costs induced by non-identical but highly similar previews are plausible, however. One possibility is that the underlying distribution of percepts is bimodal around the two stimuli shown: Sometimes the observer perceives the presaccadic stimulus to be present, sometimes the postsaccadic stimulus. Alternatively, the preview object could merely induce greater perceptual variation around the veridical postsaccadic stimulus value. This could be seen as a form of forward masking that is stronger than is found under qualitatively different preview conditions, owing to the greater similarity between both stimuli. Fig. 1 illustrates these ideas.

Identity integration, on the other hand, pertains to the situation where the perisaccadic presentation of two objects results in the postsaccadic presence of only one single object representation, such that both stimuli are not perceived as being separate or different at all. This unified transsaccadic representation may or may not still contain form properties originating from the presaccadic stimulation, depending on whether informational integration is present as well. Thus, the classical explanation of transsaccadic change detection impairments can be turned around: A failure to detect changes does not exclude the transsaccadic transfer of visual information on the relevant stimulus dimension, but might instead be the *result* of the full transsaccadic integration of the perisaccadic stimulus information, both in information contents and in identity. Two additional questions then arise: Does informational integration occur when the transsaccadic object representation is indeed singular, and if so, is identity integration also a necessary condition for this informational integration? That is, will the visual system still allow integration of detailed visual form information across saccades when, clearly, both sources of information do not originate from one continuously present object?

To address these questions, we propose three manipulations to the continuity of stimulus presentation. First, in the default condition, the presaccadic stimulus changes directly into the postsaccadic one during the saccade. We examine whether, if change detection fails under these conditions, informational integration can be observed or not. Second, we introduce a postsaccadic blanking condition, where the postsaccadic stimulus onset is delayed relative to the saccade landing. This is known to be a reliable technique to induce improved change detection performance across saccades (Deubel et al., 1996, 2002), and therefore also to induce the separate availability of two representations. At the same time, a postsaccadic blank itself induces no visual masking of the proposed detailed transsaccadic memory for object form. If identity integration is not a necessary condition for informational integration across saccades, preview effects should still be observed. Third, we introduce a condition where a visual mask is inserted during and after the saccade, prior to postsaccadic stimulus onset. If indeed transsaccadic preview effects of detailed visual form rely on a maskable visual memory trace, as we have proposed earlier, they should disappear following this manipulation.

Thus, we factorially manipulated two independent variables. The Congruency factor subsumed manipulations of the type of preview presented: Identical, Quantitatively different, or Qualitatively different. The Continuity factor on the other hand manipulated stimulus presentation into being either Continuous, Blanked, or Masked. In two separate experiments, two different dependent variables were measured. First, subjects were asked to judge whether one or two separate stimuli were present in these conditions. Note that this is not a classical change detection task, as two stimuli which might be identical but are separated by a blank or a mask could still be seen as being separate. We operationally define identity integration as the failure to detect that stimulus presentation is in reality either non-continuous or non-congruent. Second, subjects will be required to indicate their postsaccadic percept on a metrical continuum of possible stimulus shapes. In practice, we will manipulate the aspect ratio of ellipses to create this continuum. These responses will allow us to measure changes to both mean and variance of perceptual distributions in the different experimental conditions. Informational integration occurs either when an identical preview decreases the perceptual variance
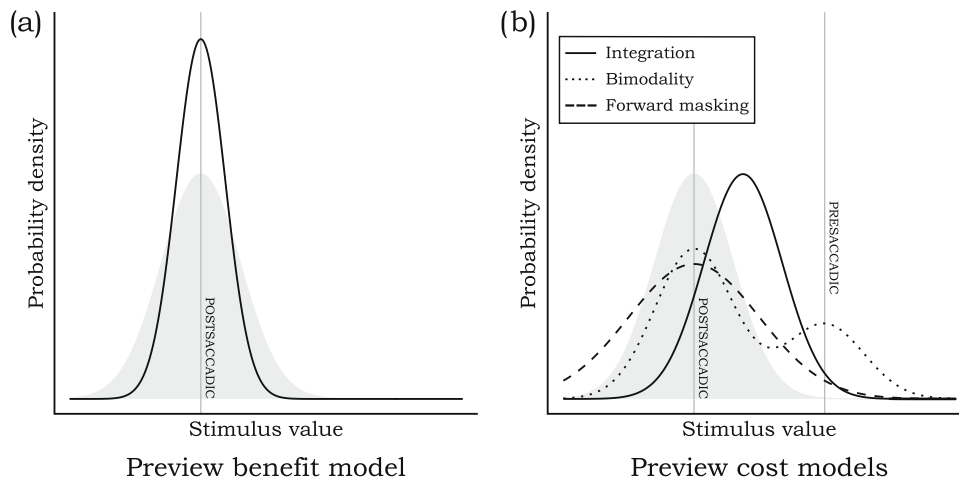
Fig. 1. (a) A model for postsaccadic recognition accuracy benefits after having glimpsed an identical presaccadic preview. The common stimulus dimension on which both the physical and the subjectively perceived stimulus values can be located is plotted against the likelihood that a particular percept will follow from a given physical stimulus presentation (vertical line). Compared to conditions without a relevant preview (shaded in grey) the variance of the distribution of postsaccadic percepts around the actual postsaccadic stimulus value is reduced. (b) Three proposed explanations for the occurrence of preview costs induced by a different but highly similar presaccadic preview, compared to a neutral baseline (shaded in gray). The Integration model (solid line) explains diminished recognition accuracy as a shift away from the postsaccadic stimulus value, towards the presaccadic stimulus value. The Bimodality model (dotted line) would hold that the presaccadic stimulus alone underlies postsaccadic perception on a proportion of the trials, leading to more incorrect responses. The Forward Masking model (interrupted solid line) proposes that an incorrect but highly similar preview increases the variability of percepts around the postsaccadic stimulus value.

compared to a qualitatively different preview, or when a quantitatively different preview induces a shift in mean towards its physical stimulus value while retaining a unimodal distribution.

2. Methods

2.1. Subjects

Five subjects participated in this study, four male and one female. One subject was author MD, the four other subjects were completely naive with respect to the aim of the study. All had normal or corrected-to-normal eyesight.

2.2. Apparatus

Stimuli were presented on a gamma-corrected Iiyama Vision Master Pro 514 22 in. CRT monitor, with a temporal resolution of 200 Hz and a spatial resolution of 800 by 600 pixels. Subjects were located at a distance of 135 cm from the experimental monitor, which subtended 17 by 13 visual degrees. Eye movement data were collected using a Dual Purkinje Image analog eye tracker (Crane & Steele, 1985), and processed by custom software on a Windows XP platform. Stimulus presentation and analog-to-digital conversion were performed by a Cambridge Research Systems Visage stimulus generator. The response buttons used were of the analog 'breaker' type, interpreting an interruption of the current as a button press, and were read in through the parallel port on the Visage.

Since phosphor persistence is a potential confound in the present study, we measured the luminance decay of the CRT monitor using a linear photodiode. While performing a display change from 'white' (83.2 cd/m²) to 'black' (<0.01 cd/m²), luminance was found to be reduced to below 10% within 4 ms, 2% within 14 ms, and 1% within 22 ms, compared to the average luminance measured over one refresh period of a white display presentation. All intrasaccadic display changes in the present study were performed at the start of a 35 ms long saccade. The relevance of phosphor persistence was further reduced by not using the full luminance range of the monitor, but rendering the stimulus contours as light-grey against a

darker grey background of 7.7 cd/m² (see Wolf & Deubel, 1997). The lightest shade of grey present at any local pixel position in any stimulus corresponded to a uniform screen luminance of 39.1 cd/m². Phosphor persistence is therefore unlikely to have had a meaningful impact on our results.

2.3. Stimuli

2.3.1. Stimulus generation

To generate our stimulus set we manipulated the aspect ratio of an ellipse, defined in polar coordinates as:

$$r = \frac{\beta}{\sqrt{1 - (\varepsilon^2 \cos^2 \theta)}}$$

where r is the radius from the center, β is the length of the short axis, ε is the aspect ratio (eccentricity) and θ is the radial angle. ε can in theory range between 0 (a circle) and 1 (long axis of infinite length). To keep the surface area of each ellipse equal at 750 square pixels regardless of its aspect ratio, β was made dependent on ε. This avoids a potentially problematic correlation between stimulus aspect ratio and overall stimulus size. A Gaussian luminance profile was used to render a smoothed contour line for each stimulus. Examples are given in Fig. 2.

2.3.2. Continuum linearization

One concern when using a parametric response continuum, as we will do, is the subjective linearity of the continuum. That is, an equal ε parameter difference between two stimuli anywhere on the continuum should yield an equal discrimination

Fig. 2. Examples from the stimulus continuum, with increasing aspect ratio. Also shown on the third ellipse from the left is the marker that indicated which response alternative the subject was currently fixating (see Procedure).

performance, regardless of their absolute positions on the continuum. It would be undesirable to have one side of the continuum allow easy discrimination between subsequent stimuli, whereas on the other end all stimuli appear to be similar despite their equidistance on the physical ε parameter continuum. To address this, we performed an intrafixation pilot experiment on three subjects. Two ellipse shapes were shown sequentially at the same central position on the screen for 200 ms each. Both stimuli were followed by a 200 ms mask, and separated by a 500 ms blank interval. Within 2000 ms after the final mask, subjects were required to respond whether the first or the second interval contained the more circular ellipse. Optimal homogeneity in discriminability across the continuum was found to occur when the ε parameter values were raised to a power P equaling 1.8. We then selected 13 stimuli that were equidistant on this transformed continuum for use in the actual experiment. Expressed as untransformed ε values, these were: 0.4500, 0.4940, 0.5348, 0.5730, 0.6092, 0.6435, 0.6763, 0.7078, 0.7382, 0.7675, 0.7958, 0.8233, and 0.8500.

2.4. Procedure

2.4.1. Practice session

In this first session, subjects practiced the saccadic eye movement and the accurate perception of postsaccadic ellipse shapes, with continuous presentation and a qualitatively different preview stimulus (see below for procedural details). Unlike in the main experiment, we manipulated the postsaccadic exposure duration to either 60, 80, 100, 120, or 140 ms. These five conditions were randomized on a trial-by-trial basis and amounted to 100 trials each. Subjects were instructed to identify the postsaccadic stimulus as being identical to one of two known ellipse shapes. That is, a simple binary response was required ('I perceived stimulus one' versus 'I perceived stimulus two'). The relevant two ellipse shapes were constant throughout this entire session and across all participants (untransformed, $\varepsilon = 0.6092$ and $\varepsilon = 0.7382$). These stimuli were specifically selected because they are symmetrical around the middle of the transformed stimulus continuum, and at a distance from each other equal to that used in the quantitatively different preview conditions of the main experiment. We aimed to have at least 85–90% correct responses for each subject at an exposure duration of 80 ms, to ensure that subjects were able of forming a sufficiently precise percept of the postsaccadic stimulus even in the condition with an uninformative preview. If a subject's performance did not meet this criterion, the postsaccadic exposure

duration for the next experiment could be individually adjusted. However, in practice this was never necessary: A postsaccadic exposure duration of 80 ms was maintained for all subjects.

2.4.2. Main experiment, part 1

All continuity and congruency manipulations were applied in a fully factorial fashion. Previews could either be qualitatively different (a square), quantitatively different (a different ellipse), or identical (the same ellipse). Postsaccadic ellipses were drawn from the entire continuum. A quantitatively different preview ellipse was always four steps to the left or to the right of the postsaccadic stimulus on this continuum. Moreover, the presentation could either be continuous, blanked intra- and postsaccadically, or first masked and then blanked intra- and postsaccadically.

Fig. 3 illustrates the timing of the events making up the different continuity conditions. At the start of each trial, subjects fixated on a cross 2.7 visual degrees to the left of the middle of the screen. Subjects could then either press the right button to perform a drift correction to the eye tracker calibration values, as long as the drift from fixation was less than one visual degree in size, or they could press the left button to start the trial. After a random fixation delay of 500–1200 ms, the presaccadic preview stimulus appeared 2.7 visual degrees to the right of the center of the screen. Subjects were required to saccade towards this stimulus within a window of 150–400 ms after its onset. Failure to do so resulted in abortion of the trial. The median saccadic latency was 187 ms, with 90% of all latencies being shorter than 252 ms. When the subject's gaze left the fixation cross, the preview was in continuous presentation conditions immediately replaced by this trial's postsaccadic ellipse. That is, trials with continuous presentation did not include panels 3 and 4 of Fig. 3. In blanked conditions a 200 ms blank display preceded postsaccadic stimulus presentation, starting as soon as saccade onset was detected (thus, not including panel 3 of Fig. 3). In masked conditions a 250 ms mask was shown from saccade onset onwards, followed by a 200 ms blank, and only then by the postsaccadic stimulus. This mask consisted of a grid of small squares of random luminance, covering an area of 1.6 by 1.6 visual degrees on the screen. The postsaccadic stimulus presentation was followed by a different random mask generated by the same procedure, for 250 ms. In this part of the experiment, subjects were to respond whether one (left button) or two (right button) distinct stimulus presentations had been present, within 2000 ms after the final mask offset. The masks were not to be considered as a stimulus presentation. During the response phase the display
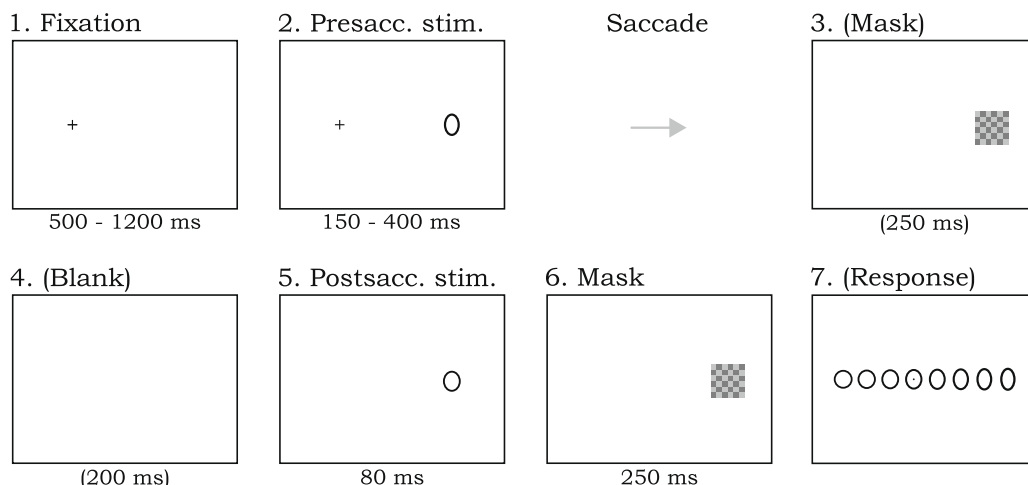

Fig. 3. Procedure for the main experiment. Stimulus presentation (panels 1–6) was identical in both parts of the main experiment, whereas the response screen (panel 7) was only present in the second part.

remained blank. Only one out of nine possible conditions should for a perfect observer yield the response 'one presentation' (continuous presentation, identical preview). Subjects were informed that the majority of responses would be in the 'two presentations' category, but were not told their exact proportion. No feedback was given.

Per condition 50 trials were collected, for a total of 450 trials in one 1-h session. Conditions were randomized across the entire experiment on a trial-by-trial basis. Blocks consisted of 50 different trials each, after which subjects could rest. At the end of each block aborted trials were recycled. Twice aborted trials were not recycled again. In total, 4.84% of trials was aborted twice and thus excluded from the analysis.

2.4.3. Main experiment, part 2

Here, stimulus presentation was exactly identical to the first part of the main experiment, but the required response was different. Subjects were instructed to remember the postsaccadic stimulus form, and locate it on a continuum consisting of eight ellipses (see Fig. 3, panel 7). In addition, they were told that in case two consecutive ellipses had been perceived, they should make the effort to report the percept of the second ellipse in isolation. They were also informed that the postsaccadic stimulus shown was always present on the response continuum, and that each location on the response continuum was equally likely to contain the postsaccadic stimulus. Both of these pieces of information were, in fact, true. Subjects could select their response through eye movements, marking the continuum location they were fixating with a central dot (see Fig. 2), and confirm their response by pressing the left response button.

The continuum shown during the response phase was a contiguous subset of eight from the entire continuum of 13. It was rendered as a single row of stimuli in the middle of the screen. The same eight locations on the screen were always used to render the eight response alternatives, irrespective of the specific subset of stimuli that was shown, starting with the more circular ellipse at the first position. The postsaccadic stimulus which was actually presented was equally likely to occur at each of these eight positions. In case of a quantitatively different preview, an ellipse four steps away from the postsaccadic stimulus was selected to be the presaccadic stimulus. Because we required the presaccadic stimulus to also be selectable on the visible response continuum, this made the presaccadic stimulus identity follow deterministically from the combination of the specific subset of stimuli displayed and the postsaccadic stimulus identity: If the postsaccadic stimulus was on response locations 1–4, a quantitatively different preview stimulus would be less circular by four steps on the response continuum, whereas if the postsaccadic response stimulus was on response locations 5–8, it would be more circular by four steps.

Nine hundred trials were collected across three 1-h sessions per subject, with conditions randomized on a trial-by-trial basis. Blocks consisted of 50 trials, after which subjects could rest. A total of 4.13% of trials was aborted twice and excluded from the analysis. Saccadic latencies had a median of 178 ms, and were shorter than 217 ms on 90% of all trials. Response times had a median of 3.4 s, and were shorter than 4.9 s on 90% of all trials.

3. Results

3.1. Main experiment, part 1

Fig. 4 shows the average responses to the task. Clearly, non-continuous trials were always seen as two distinct presentations, whereas for continuous trials this was only the case when the pre-
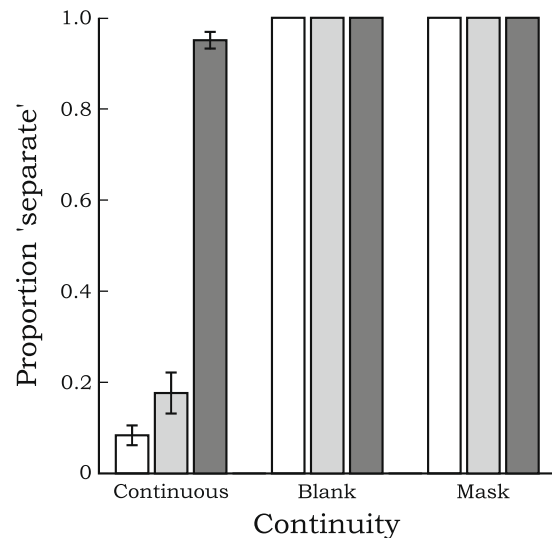

Fig. 4. Average results for part 1 of the main experiment. Bars from light to dark denote performances with identical, quantitatively different, and qualitatively different previews respectively. Error bars indicate one standard error of subject variability. Non-continuous trials were always easily seen as two separate stimuli; for continuous trials this was only the case when the preview was qualitatively different.

view was qualitatively different. The results for continuous, identical preview trials show that subjects displayed an average false alarm rate of 8.4% even when there was in reality no discontinuity or incongruency in presentation. Trials with a quantitatively different preview were reported to consist of two separate stimulus presentations in only 17.6% of cases. Based on the paired logit difference between both conditions in each subject, and its variability across subjects, the performance increase compared to identical preview trials is significant at the population level ($t(4) = 2.23$, $p = 0.04$). However, the absolute increase in the number of 'two presentations' responses remains low.

3.2. Main experiment, part 2

Before continuing to the main analysis, attention must be drawn to an important property of our methodological approach. In order to allow both the presaccadic and the postsaccadic stimulus of trials with a quantitative stimulus difference to be valid response alternatives, their intermediate stimulus could never be near the extremities of the response continuum. This avoids an important pitfall: Subjects perceiving only the presaccadic stimulus could otherwise on some trials, where the presaccadic stimulus is not shown on the response continuum, be forced to respond with the closest visible alternative – an intermediate stimulus. However, a new but controllable problem now arises: Should the subject display a pure response bias away from the extremities of the continuum, then he or she will give a higher relative proportion of intermediate responses than when no such bias was present, and as a result will appear to have an average percept inclined towards the presaccadic stimulus value.

Fig. 5 illustrates that a response bias is indeed present in our data: Subjects preferentially responded with the more circular response alternatives, and importantly, shunned away from the extremities of the continuum even when no quantitatively different preview was present. Thus, an effect of a quantitatively different preview manifesting itself as a shift of the mean percept towards the presaccadic stimulus value only indicates the presence of a true preview effect when it significantly exceeds the shift in mean percept that can be attributed to the response bias. To
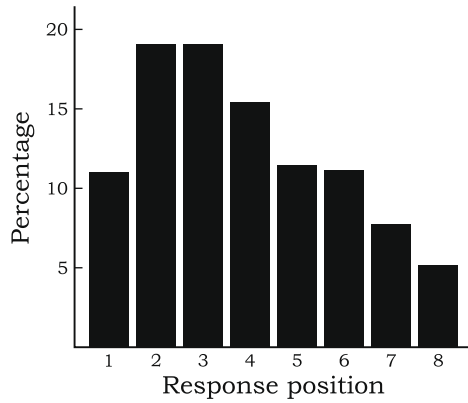
Fig. 5. Distribution of responses in conditions without a quantitatively different preview. A bias towards the more circular and away from the extreme response positions can be noted. The distribution of the actually presented postsaccadic stimuli across the response continuum is flat.

gories according to the actual or virtual direction of the preview ellipse on the continuum, compared to the postsaccadic ellipse: 'The preview was more circular' (the postsaccadic stimulus was on response positions 5–8) or 'the preview was less circular' (the postsaccadic stimulus was on response positions 1–4).

Fig. 6 shows the mean responses across all subjects for all conditions, expressed as the distance on the response continuum between the stimulus that was actually presented in the postsaccadic interval, and the stimulus that was selected by the subject as having been presented. A within-subjects analysis of variance (ANOVA) revealed significant effects for Direction of preview ($F(1, 4) = 364.42$, $p < 0.01$), the two-way interactions between Direction and Congruency ($F(2, 8) = 82.30$, $p < 0.01$) and Direction and Continuity ($F(2, 8) = 25.90$, $p < 0.01$), and the three-way interaction between Direction, Congruency, and Continuity ($F(4, 16) = 13.61$, $p < 0.01$). An effect of preview direction (whether actual or virtual) is indeed apparent in all conditions; however, it is much larger on trials with a quantitatively different preview. This effect is strongest on continuous trials, is diminished considerably on blanked trials, and absent entirely when stimulus presentation is interrupted with a mask. This is corroborated by separate ANOVAs on the different Continuity conditions; the Direction by Congruency interaction remains significant for continuous trials ($F(2, 8) = 59.05$, $p < 0.01$) and blanked trials ($F(2, 8) = 117.91$, $p < 0.01$), but is insignificant for masked trials ($F(2, 8) = 1.63$, $p = 0.26$). Excluding Masked trials from the overall analysis does not change the significance of the three-way interaction
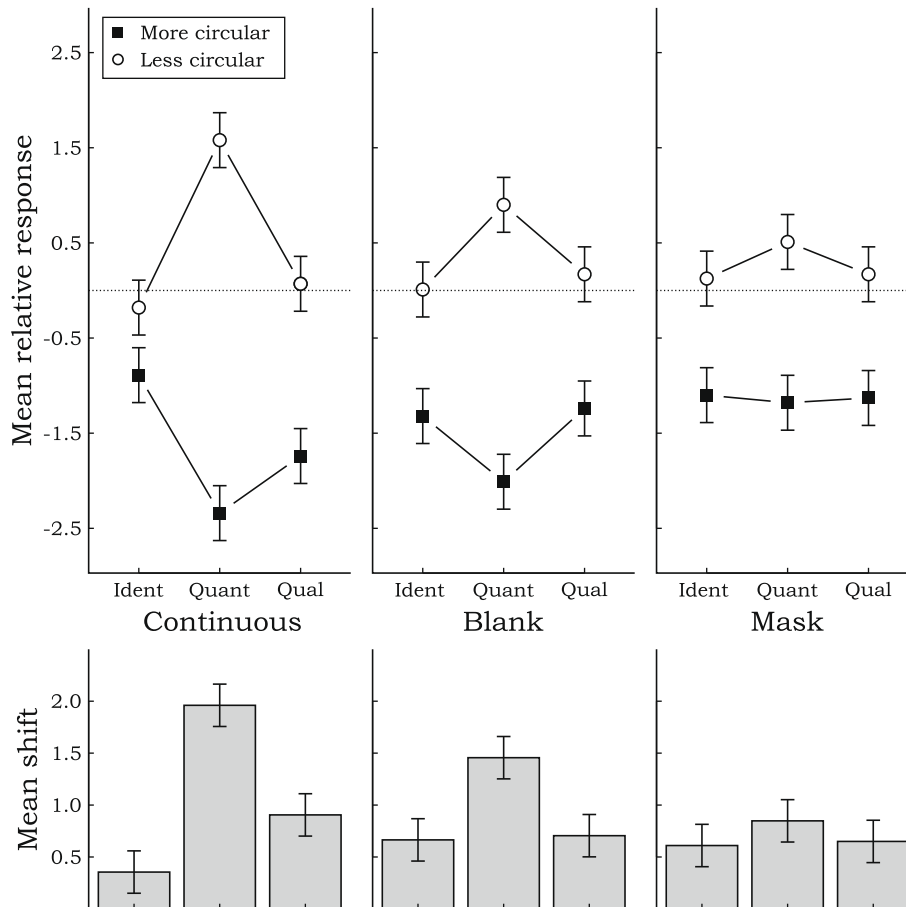
measure this baseline effect, we split up the data for identical and qualitatively different preview conditions as if a quantitatively different preview had been present. This is made possible by the fact that, as we noted above, the location of a quantitatively different preview stimulus on the response continuum is deterministic given the position of the postsaccadic stimulus. We could therefore divide the trials of all conditions in the experiment into two cate-

Fig. 6. Top: Mean responses for all conditions, split up by actual or virtual direction of the preview stimulus compared to the postsaccadic stimulus value. The dotted line indicates a perfect response unaffected by preview information or response biases, and error bars denote one standard error of subject variability. Bottom: The resulting average shift in mean percept towards the relative preview stimulus value (which equaled ±4), compared to the mean for both preview stimulus directions. Error bars again denote one standard error of subject variability.
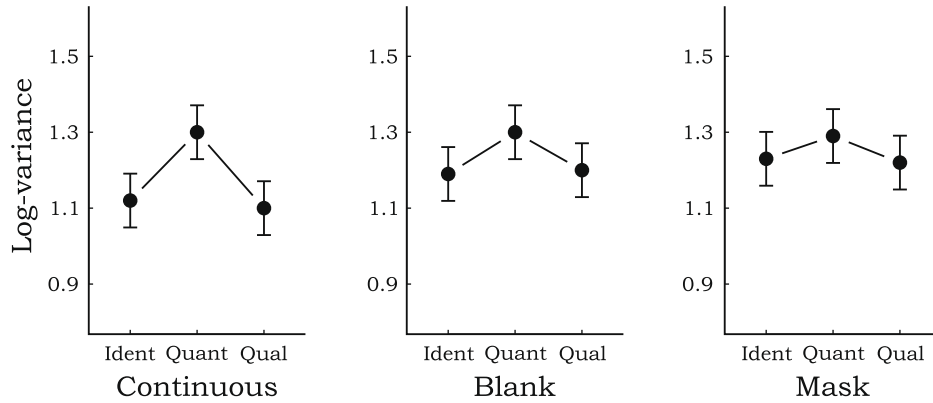
Fig. 7. Average log-variance estimates for responses in all conditions. No significant differences were present in an overall ANOVA. Error bars denote one standard error of subject variability.

$(F(2, 8) = 15.07, p < 0.01)$, demonstrating that the strength of preview effects does indeed differ between continuous and blanked trials alone as well. A Tukey HSD post-hoc comparison between all means reveals that the baseline measurement of shift in mean percept, i.e. excluding conditions with an actual quantitative difference between both stimuli, contains two outliers at a 5% significance level: In the continuous conditions with more circular virtual previews (lower-left line in the graphs), identical previews suffered significantly less from the bias away from the extremes than some of the other conditions, whereas the qualitatively different preview condition appeared to be most inclined towards the preview stimulus. All other baseline measurements for a given

Direction are statistically indiscernible. Fig. 7 shows the average response precision expressed as log-variances of the responses around their mean values in each condition. Again, the data were split up by actual or virtual preview direction, obtaining two variance estimates for each of the nine experimental conditions. This is necessary to allow a valid comparison between quantitatively different and other conditions. Both estimates were, per subject, pooled into one number per experimental condition. A within-subjects ANOVAVA (Analysis of Variance of Variance, Lederman & Taylor, 1972) was then performed on the log-transforms of these variance estimates. However, no significant effects for either Continuity $(F(2, 8) = 1.62, p = 0.18)$, Congruency $(F(2, 8) = 0.28,$
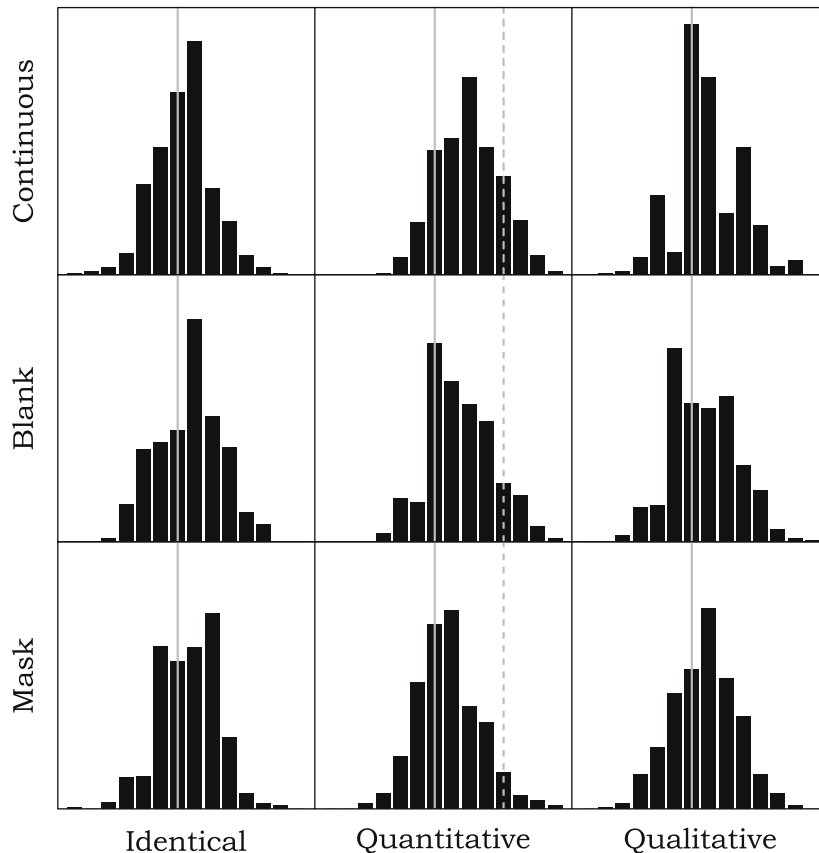

Fig. 8. Histograms of response behavior, pooled across preview direction and across subjects. Full lines indicate the postsaccadic stimulus value, dotted lines the presaccadic stimulus value (when applicable).

$p = 0.72$) or their interaction ($F < 1$) could be found. Thus, response precision could not be shown to vary systematically across conditions. Fig. 8 shows the raw histograms for each condition, summed across both preview directions. These contain the same information on mean and variance of the perceptual distributions as the previous two graphs, and in addition demonstrate the response distributions to be unimodal. Both for quantitatively different previews on continuous trials, where subjects could generally not detect the presence of two different stimuli, and on blanked trials, where they could, a single distribution appears to underlie the shift in mean percept towards the preview stimulus rather than a bimodal distribution around the two stimuli actually displayed.

Finally, exploring the response times, the main effects of Continuity ($F_{(2, 8)} = 1.96$, $p = 0.20$) and Congruency ($F < 1$) were not significant, nor was their interaction ($F < 1$).

4. Discussion

The results obtained in the quantitatively different preview conditions allow three main conclusions. First, detailed and precise presaccadic information is not only carried across the saccade (Demeyer et al., 2009; Deubel et al., 1996, 2002), but also enables true informational integration of visual form: A unimodal distribution of percepts with a mean intermediate to the two stimuli actually shown is observed. Second, this informational integration can occur, and indeed occurs in its strongest form, when both stimuli are not perceived as being separate entities. This implies that the often-made assumption that a failure to detect stimulus changes must either stem from a failure to carry sufficiently precise visual detail across the saccade or from an immediate loss or suppression of this information at postsaccadic stimulus onset, is in fact incorrect. Instead, informational integration and identity integration can go hand in hand. However, at the same time identity integration is not a necessary condition for informational integration, as the latter can also be observed under postsaccadic blanking conditions, when both stimuli are clearly perceived as being separate. One cause for the weaker preview effects observed in blanking conditions could be an ongoing decay of the relevant transsaccadic memory for visual form during the blank interval. Third, this relevant transsaccadic memory is visually maskable.

In case of identical previews, however, we failed to observe informational integration in the form of improved response precision in any continuity condition. Only a weak indication of a more reliable postsaccadic percept following an identical preview was present in the data: Continuous identical previews suffer significantly less from the observed response bias away from the extremes that we observed, when compared to rest of the identical or qualitatively different preview conditions. The absence of clear preview effects on the variability of responses is at odds with our previous finding of more accurate and faster postsaccadic identification following an identical presaccadic preview. Possibly, the response method employed in the present study induces a systematic overestimation of the actual postsaccadic perceptual uncertainty when compared to a postsaccadic identification task requiring a binary response. Indeed, selecting an ellipse shape on the response continuum requires time, as well as the reviewing of several only subtly different shapes and the execution of additional saccades. Moreover, the postsaccadic percept might be less efficiently located within a range of physically present stimuli than they are matched with existing memory representations. Subtle differences in perceptual precision as a result of preview manipulations could therefore be swamped by a general performance degradation introduced by the response method. However, the absence of response time effects in the data indicates that the response selection process did not differ between the various congruency conditions.

In addition to integration of visual detail, some transsaccadic interaction between qualitatively different stimulus form properties might also be present in the data. On continuous trials with a qualitatively different preview a stronger shift in perceptual mean occurs than in the other baseline conditions, though still not nearly as strong as in quantitatively different preview conditions. The point here is that while such a square preview is not compatible with an ellipse for contour integration, the square preview does have a specific aspect ratio equaling 1. Fig. 6 clearly shows, indeed, that the effect exclusively occurs when the virtual preview would have been more circular, though it disappears when a blank or masks interrupts presentation. Potentially, the metrical properties of qualitatively different preview stimuli might somehow still interact with postsaccadic form processing, albeit weakly and within a more limited temporal window following saccade landing. Further research would however be needed to characterize this effect better.

The transsaccadic visual analog. These results are consistent with the notion that transsaccadic persistence of visual information is not only supported by VSTM, but also by a highly detailed, quickly decaying and visually maskable memory trace of the presaccadic stimulus display. Previous supporting evidence of the existence of such a transsaccadic visual memory store has been sparse, but not absent (Hayhoe, Lachter, & Feldman, 1991; McRae, Butler, & Popiel, 1987; Palmer & Ames, 1992). De Graef and Verfaillie (2002) have suggested that this memory trace is the transsaccadic version of the Visual Analog (VA; see also Irwin & Yeomans, 1986). Contrary to the integrative visual buffer proposed by McConkie and Rayner (1976), however, we suggest that the transsaccadic VA does not just store a carbon copy of the retinal input information. The visual representations relevant to the transsaccadic VA have already gone through a fair amount of visual processing, and have been stripped of low-level stimulus properties such as luminance, contrast or local detail. Instead, they describe behaviorally relevant, object-based visual aspects of the stimulus such as its detailed form. This view is consistent with psychophysical (Melcher, 2005, 2007) as well as neurophysiological (Merriam, Genovese, & Colby, 2007; Nakamura & Colby, 2002) findings demonstrating that in extrastriate but not striate visual cortex, receptive fields of retinotopic visual neurons are routinely remapped according to the saccadic displacement of the projected retinal image. In these areas, as well as in temporal cortex, object form representations can persist for hundreds of milliseconds after stimulus offset provided that no strong backward visual mask is present (Keysers, Xiao, Földiák, & Perrett, 2005; Landman, Spekreijse, & Lamme, 2003, 2004; Sligte, Scholte, & Lamme, 2008, 2009). In addition, this explains why transsaccadic integration of visual detail does not have the undesirable effect of introducing the peripheral blur into foveal vision: Through the mid-level encoding of visual stimulation across saccades, the visual system abstracts such image-like qualities as 'blur' from the stimulus, and creates a common representational ground for visual integration across different spatial resolutions.

It is important to note that stimulus persistence in the VA is not visible, but informational in nature. That is, the observer has no visual experience emanating from the presence of information in the VA (Coltheart, 1980). In addition, the contents of the VA are not directly accessible for conscious recollection, but must be selectively and attentively encoded into a more durable memory store, such as VSTM, in order to be explicitly retrieved. This resulting VSTM representation is then what underlies the task response, and what allows such response to be given beyond the VA's normal decay time and despite the presence of subsequent visual stimulation. Although we have previously stated that VSTM is preferentially

focused on encoding structural and categorical information, it is also capable of storing detailed visual form information on a single object if the task requires such, and if enough time is available to complete its selective read-out from the VA (for a recent study see Salmela, Mäkelä, & Saarinen, 2010). This read-out time could then precisely be what an immediate postsaccadic blank provides in transsaccadic change detection tasks, and what allows the explicit postsaccadic availability of a more precise representation of the contents of the presaccadic display (De Graef & Verfaillie, 2002; Germeys, De Graef, Van Eccelpoel, & Verfaillie, submitted for publication).

We speculate that informational integration of visual form, as observed in the present study, occurs on the basis of informational persistence in the transsaccadic Visual Analog. Identity integration, on the other hand, we equate with the separate availability of both stimuli in VSTM. When the immediate postsaccadic stimulation is sufficiently similar to the limited read-out of the presaccadic stimulus already available in VSTM, we propose the visual system will continue to fill the same VSTM slot with more detailed – now integrated – information from the VA, resulting in a single unified transsaccadic percept. If not, a second VSTM slot will be opened for the representation of the postsaccadic object, and two separate stimuli will be perceived. Note that this view also resolves the apparent contradiction that integration and masking of visual form representations occur across each trial's main saccade, whereas the representation underlying the response is virtually incorruptible by the execution of additional saccades to additional ellipses during the response selection phase. Under the theoretical assumption that the VA underlies the transsaccadic integration process whereas VSTM underlies the response, this is easily understood.

5. Conclusions

Thus, parametric information on object form is not only retained, but also integrated across fixations. Unlike transsaccadic fusion models of the past, we propose that this happens at an intermediate level of visual representation at which low-level properties of the visual image have already been abstracted. Informational integration across saccades was shown to be strongest under conditions of identity integration, when pre- and postsaccadic stimuli could not be discerned as being two separate objects. It was attenuated by an intervening postsaccadic blank interval, and removed by an intervening mask. However, in the case of identical preview conditions, we could not observe a reduction in perceptual variance as a result of this integration process. We propose that these effects are to be explained by the involvement of a highly detailed and precise maskable memory store in transsaccadic vision – the transsaccadic Visual Analog.

Acknowledgments

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