



Object form discontinuity facilitates displacement discrimination across saccades

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Object form discontinuity facilitates displacement discrimination across saccades

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Abstract

Stimulus displacements coinciding with a saccadic eye movement are poorly detected by human observers. In recent years, converging evidence has shown that this phenomenon does not result from poor transsaccadic retention of presaccadic stimulus position information, but from the visual system's efforts to spatially align presaccadic and postsaccadic perception on the basis of visual landmarks. It is known that this process can be disrupted, and transsaccadic displacement detection performance can be improved, by briefly blanking the stimulus display during and immediately after the saccade. In the present study, we investigated whether this improvement could also follow from a discontinuity in the task-irrelevant form of the displaced stimulus. We observed this to be the case: Subjects more accurately identified the direction of intrasaccadic displacements when the displaced stimulus simultaneously changed form, compared to conditions without a form change. However larger improvements were still observed under blanking conditions. In a second experiment, we show that facilitation induced by form changes and blanks can combine. We conclude that a strong assumption of visual stability underlies the suppression of transsaccadic change detection performance, the rejection of which generalizes from stimulus form to stimulus position.

Keywords: eye movements; visual stability; transsaccadic perception; saccadic suppression

Word count: 190

1. Introduction

As human observers make saccadic eye movements to explore a scene, its projection on the retina is subject to large shifts of various directions and sizes. Despite the challenge which this succession of lateral input displacements would seem to pose to the visual system, observers are provided with a subjective experience of a stable and richly detailed world. This intriguing behavior and the mechanisms underlying it have received ample attention from vision scientists.

Intuitively, the visual system would seem to possess all necessary information to stabilize perception across eye movements, since the motor signals which drive saccades are initiated from within the same biological system that has to compensate for the visual input displacements produced by them. If the *extra-retinal* motor signal of the eye movement is simply subtracted from the *retinal* displacement signal of an unmoving object, a spatially stable and therefore veridical percept could ensue. This suggestion of a cancellation approach to the visual stability problem is indeed an old one (von Helmholtz, [1866](#); Sperry, [1950](#); von Holst & Mittelstaedt, [1950](#)), but on a neurophysiological level both types of signals are too different to be simply subtractable (Sommer & Wurtz, [2008](#)). Rather, the currently most popular theory holds that a corollary discharge of the saccadic motor signal is indeed present, but serves a different purpose: By briefly shifting the receptive fields of retinotopic neurons in anticipation of the change in correspondence between the retinotopic and spatiotopic coordinate systems, the same neurons can transsaccadically encode information on the same parts of a scene despite the retinal image shift induced by the eye movement. Such receptive field remapping has been observed in parietal cortex, extrastriate visual cortex, the frontal eye fields, and the superior colliculus; using single-cell recording, ERPs, fMRI, or psychophysical studies; and both in monkeys and in humans (Duhamel, Colby, & Goldberg, [1992](#); Mathôt & Theeuwes, [2010](#); Melcher, [2005](#), [2007](#); Merriam, Genovese, & Colby, [2003](#), [2007](#); Nakamura & Colby, [2002](#); Parks & Corballis, [2008](#); Umeno & Goldberg, [1997](#); Walker, Fitzgibbon, & Goldberg,

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3 [1995](#)). Note however that horizontal activation transfer between neurons encoding a salience map could
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5 constitute an alternate explanation to some of these data (Cavanagh, Hunt, Afraz, & Rolfs, [2010](#)).
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10 It seems unlikely that any mechanism compensating for the retinal image shift through extra-retinal
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12 information alone could fully account for the human perceptual experience of visual stability though, as
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14 the corollary discharge signal and the processes it drives are clearly not free of noise and biases. When
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16 briefly flashing isolated stimuli in darkness around the time of a saccade, significant errors have been
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18 observed to occur in their localization. Starting up to 100 ms before the initiation of the eye movement
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20 perceived locations are biased in the direction of the saccade, whereas an opposite tendency is present at
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22 the end of the saccade and for several tens of milliseconds afterwards (Honda, [1989](#), [1991](#)). Moreover,
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24 when stimuli are flashed before the saccade and in the presence of visual references, human localization
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26 data display not only a lateral bias but also a compression of visual space onto the saccade target (Lappe,
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28 Awater, & Krekelberg, [2000](#); Ross, Morrone, & Burr, [1997](#)). Perisaccadic localization errors thus appear
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30 to vary in both direction and magnitude across space and time, and can be observed to be present during a
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32 significant part of the successive fixation periods. If the extra-retinal mechanisms relevant to especially
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34 the lateral shift component of perisaccadic localization behavior would also be driving the stabilization of
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36 real-life vision, absolute space perception would indeed be non-veridical during the majority of the time
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38 spent exploring a scene. Therefore, the corollary discharge theory of visual stability merely shifts the
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40 problem. Rather than having to account for the lack of large apparent scene displacements with every
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42 saccade made, we are now left to wonder why observers have no experience of smaller instabilities as a
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44 result of both transient and absolute errors in compensating the retinal effects of the saccadic motor
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46 command.
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50 51 52 53 *Change detection across saccades*

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55 Corroborating this conclusion, actual external instabilities in the form of stimulus displacements applied
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57 during a saccade go largely unnoticed to the observer, especially when the saccade length is long
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3 (Bridgeman, Hendry, & Stark, [1975](#); Li & Matin, [1990](#)). This implies that there is no need for a perfect
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5 extra-retinal compensation mechanism, since the visual system is apparently able of resolving
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7 transsaccadic instabilities even when they do not result from an eye movement but merely coincide with
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9 one. The interpretation of these results has often been in terms of the precision with which presaccadic
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11 information is encoded and transferred across the saccade, suggesting a coarse transsaccadic
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13 representation of positional information (Bridgeman, Van der Heijden, & Velichkovsky, [1994](#); Irwin,
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15 [1992](#); O'Regan, [1992](#)). The argument then is that we do not perceive stimulus displacements across
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17 saccades because we do not have a sufficiently accurate postsaccadic representation of presaccadic
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19 stimulus position information. This interpretation is congruent with a second class of experimental results,
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21 demonstrating that transsaccadic change detection of stimulus form is similarly impaired (Deubel,
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23 Schneider, & Bridgeman, [2002](#); Grimes, [1996](#); Henderson & Hollingworth, [2003](#)), and that only coarse
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25 and abstract form properties of presaccadic stimulation contribute to the speed and accuracy of
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27 postsaccadic stimulus recognition (Henderson, [1994](#), [1997](#); Pollatsek, Rayner, & Collins, [1984](#); Pollatsek,
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29 Rayner, & Henderson, [1990](#); Rayner, McConkie, & Zola, [1980](#)).

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36 Change detection across saccades is not always severely impaired, however: Stimuli that are defined by
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38 their orientation (Pollatsek & Rayner, [2002](#); Verfaillie, De Troy, & Van Rensbergen, [1994](#)), embedded in
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40 a configuration (Verfaillie, [1997](#); Verfaillie & De Graef, [2000](#)) or moving (Gysen, Verfaillie, & De Graef,
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42 [2002](#)) allow better task performance. One explanation could be that some aspects of a scene or an object
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44 are simply more accurately represented than others. But as Mitroff, Simons, and Levin ([2004](#)) point out,
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46 absent change detection does not necessarily imply the absence of a representation that could in principle
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48 enable successful task completion: It only demonstrates that such a representation is not being employed.
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50 That is, the visual system may be unable to adapt to the artificial demands of a psychophysical task.
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52 Indeed, the priority of real-life transsaccadic perception would seem to be upholding subjective stability
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54 rather than accurately detecting highly unlikely and behaviorally irrelevant events, such as minor object
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56 displacements which are exactly synchronized with a saccade. As a result a detailed stimulus position
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3 representation could be suppressed from conscious perception despite the explicit instruction to retrieve it.
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5 It could however still be covertly employed for other purposes, such as motor coordination (Prablanc &
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7 Martin, [1992](#)).
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10 11 *Blanking and landmark effects*

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13 Deubel, Schneider, and Bridgeman ([1996](#)) delivered the most convincing evidence for this idea. In their
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15 study, subjects were required to indicate the horizontal displacement direction of a small dot, when
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17 performed intrasaccadically. Predictably, task accuracy was low for stimulus shifts of up to two visual
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19 degrees in size. However, the simple insertion of a short blank interval during and immediately after the
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21 saccade, before the onset of the postsaccadic stimulus, improved displacement discrimination performance
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23 dramatically. This strongly suggests that the presaccadic position representation was indeed detailed
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25 enough to solve the task, but without an immediate postsaccadic blank this representation could not be
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27 explicitly compared to the incoming postsaccadic position information, or at least not in a veridical
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29 manner.
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35 Deubel, Bridgeman, and Schneider ([1998](#)) further report that if a spatially stable but postsaccadically
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37 blanked stimulus was displayed in the vicinity of an intrasaccadically displaced but continuously present
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39 second stimulus, the latter stimulus was seen as stable and used as a reference for inferring the apparent
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41 displacement of the former. These findings indicated that the encoded presaccadic position information is
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43 not merely being suppressed, but actively being used in a visual stability mechanism based on retinal
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45 information: Assuming that the real world is stable, presaccadic and postsaccadic vision will be aligned
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47 with one another based on transsaccadically persistent landmarks. Only when this is not possible, for
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49 instance when the visual system does not encounter any immediate stimulation after a saccade, will it fall
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51 back on different mechanisms of visual stability, that are presumably extra-retinal and based on the
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53 corollary discharge. The fact that this fallback to imperfect position information actually improves task
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55 performance demonstrates the strength of the visual stability assumption. Thus, while extra-retinal
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3 information can certainly contribute to the stability of transsaccadic vision, visual information is
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5 dominant. This precedence of vision over conflicting information sources has also been called ‘visual
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7 capture’ (Matin, Picoult, Stevens, Edwards, Young, & MacArthur, [1982](#)).
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10 11 *The role of object form in attaining visual stability*

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13 Surprisingly, Deubel et al. ([2002](#)) report that landmark effects do not require form similarity between the
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15 presaccadic stimulus and its corresponding postsaccadic landmark. To be exact they observed that the
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17 performance improvements induced by target blanking can be undone by inserting flanking stimuli around
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19 the position of the displaced saccade target during the blank interval, as long as these flankers are clearly
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21 localized within the spatial dimension on which the saccade displaces the retinal projection (e.g., long
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23 horizontal bars will not work for a horizontal saccade). Similarly, Koch and Deubel ([2007](#)) demonstrate
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25 that the landmark effect can go as far as using the gravitational center of two postsaccadic objects as a
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27 spatial reference for the position of a single presaccadic stimulus. Thus, when the target object is not
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29 available immediately after the saccade, other nearby objects can be used as a reference even if they were
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31 not present before the saccade. Their position on the spatial dimension traveled by the saccade will then be
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33 assumed to correspond to that of the saccade target.
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40 This appears to run counter to the notion of a stable world null hypothesis as the main determinant of
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42 visual stability in real-life vision. Indeed, it has been suggested but never proven that the visual stability
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44 assumption is primarily evaluated by attempting to relocate the saccade target object itself on the basis of
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46 certain critical locating features immediately after saccade landing (Deubel, Wolf, & Hauske, [1984](#);
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48 McConkie & Currie, [1996](#)). In the study of Deubel et al. ([2002](#)) the saccade target object was however
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50 absent when the saccade landed, possibly invoking a separate visual stability mechanism which could
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52 utilize flanking landmarks (Higgins & Wang, [2010](#)). In the present study we will therefore investigate
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54 whether displacement detection can be observed to be improved when the saccade target does remain
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56 present at saccade landing, but is unstable in its form properties as well as its position.
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3 Looking at this research premise from a somewhat different angle, Deubel et al. (2002) also show that an
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5 immediate postsaccadic blank improves transsaccadic detection performance for form changes as well as
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7 displacements. This suggests that a similar mechanism could be underlying both types of saccadic change
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9 detection suppression, encompassing an assumption of visual stability that is maintained and used as a
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11 basis for a transsaccadically stable perceptual experience as long as the discrepancy between both
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13 perisaccadic pieces of information can reasonably be assumed to be the result of an error internal to the
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15 human body (Niemeier, Crawford, & Tweed, 2003). If the rejection of such an inbuilt assumption of
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17 visual stability is the key to detecting intrasaccadic stimulus changes of both object position and object
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19 form, could then indeed the successful detection of an object form change be sufficient to refute visual
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21 stability and improve detection of simultaneous displacements of the same object? Or, to make a perhaps
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23 counterintuitive prediction: Is displacement detection across saccades easier between dissimilar stimuli?
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29 To test whether a rejection of visual stability generalizes from form to position, we asked subjects to judge
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31 the direction of saccade target displacements while the task-irrelevant visual form of the saccade target
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33 could be altered simultaneously. In addition, we compared the effect of a form change to the effect of a
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35 postsaccadic blank, the most commonly used technique to induce better displacement discrimination
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37 performance. If both manipulations trigger the same mechanism of disrupting visual stability, we would
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39 expect them to have similar but non-additive effect sizes. That is, if a postsaccadic blank has already
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41 refuted the visual stability assumption, a form change to the re-appearing saccade target will do nothing to
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43 improve performance further. If on the other hand they activate independent mechanisms of performance
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45 facilitation, they should be additive.
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51 In sum, four questions were initially asked:

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53 1. Does a postsaccadic blank improve intrasaccadic displacement discrimination in our paradigm?
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55 2. Does a form change to the saccade target improve displacement discrimination?
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3. Is displacement discrimination performance improved to the same degree by a postsaccadic blank and an intrasaccadic form change?
4. Does their joint occurrence lead to an additive effect?

2. Experiment 1

2.1 Methods

2.1.1 Subjects

Six subjects, five male and one female, between the ages of 24 and 47 participated in this experiment. Two of these subjects were authors on this paper; the remaining four subjects were completely naive with regard to the aims and conditions of the experiment. All had normal or corrected-to-normal vision.

2.1.2 Apparatus

Stimuli were presented on an Iiyama Vision Master Pro 541 22 inch monitor, with a temporal resolution of 200 Hz and a spatial resolution of 800 by 600 pixels, subtending 17 by 13 visual degrees. Participants were seated at a distance of 135 cm from the monitor, with their head stabilized by a head rest and a bite bar with dental impression compound. Eye movement data were collected using an analog Dual Purkinje Image eye tracker (Crane & Steele, [1985](#)) sampled at 1000 Hz, 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. The monitor was gamma-corrected by the automatic routines included with the Visage system.

PLACE FIGURE 1 AROUND HERE

2.1.3 Stimuli

We used four simple geometrical shapes as stimuli, to make form changes as qualitative as possible while still retaining easy identification of their centers. This enables subjects to accurately detect displacements even between dissimilar shapes. The shapes were a cross, a circle, a square, and a diamond (see Figure 1). They subtended an area of 26 by 26 pixels (0.55 by 0.55 visual degrees on the screen). The intrasaccadic location changes performed relative to the center of each stimulus ranged from 0.11 to 0.44 visual degrees, resulting in an overlap between 0.06 and 0.44 visual degrees. A background monitor luminance of 7.7 cd/m² and a Michelson contrast of 0.71 were used for all stimuli.

2.1.4 Procedure

We used a three-way fully factorial design. First, we manipulated the size of the saccade target displacement to either 0.11, 0.22, 0.33 or 0.44 visual degrees. A vertical displacement (upward or downward) was chosen in order to avoid introducing a systematic bias related to the horizontal undershooting of the saccade target. Second, on half of the trials we introduced a postsaccadic blank, on the other half we did not. Third, we changed the stimulus form on half of the trials. All 12 combinations of possible stimulus form changes (cross-to-circle, square-to-diamond, etc.) were used randomly.

PLACE FIGURE 2 AROUND HERE

Figure 2 illustrates the procedure. In a dimly lit room, participants were instructed to fixate a small cross 2.7 degrees to the left of the center of the screen. They had two buttons at their disposal. During fixation, they could press the right button to instantly apply drift correction to the eye tracker calibration setup, as long as the deviation was smaller than one visual degree of angle. In the beginning of the experiment, the experimenter gave the explicit instruction to use the drift correction button when the fixation position was

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3 found to be inaccurate, but after the first block most subjects started using it spontaneously following a
4 failed fixation. As soon as the left button was pressed, a random fixation period lasting between 500 and
5 1500 ms started, after which a stimulus appeared 5.4 degrees to the right of fixation, 2.7 degrees to the
6 right of the center of the screen. When fixation on the initial cross was insufficiently accurate (eye
7 position outside a region of 0.5 by 0.5 degrees enveloping the fixation cross, plus a 0.3 degree tolerance
8 zone to each side), the trial was aborted and the subject was admonished with both a visual and an
9 auditory signal. In the vertical direction, the center of presaccadic stimulus could be located up to 0.33
10 degrees away from the center of the screen, either upwards or downwards. Subjects were instructed to
11 saccade towards the presaccadic stimulus as quickly as they could. Saccade latencies shorter than 150 ms
12 and longer than 400 ms resulted in an abortion of the trial. In practice, the mean saccade latency was 188
13 ms, and on 95% of all trials it was shorter than 250 ms. Once the saccade was initiated and the gaze left
14 the fixation zone, the stimulus was immediately displaced and could either disappear (blinking
15 conditions) or not, and/or change form (form change conditions) or not. We estimate the intrasaccadic
16 stimulus changes to have become effective on the screen 10-15 ms into the saccade. The center of the
17 postsaccadic stimulus was never more than 0.22° removed from the horizontal centerline of the screen,
18 and every postsaccadic stimulus position was equally likely to have resulted from an upward or a
19 downward displacement. This way, postsaccadic position information was by itself not informative to
20 solve the task. A blank lasted 100 ms, after which the postsaccadic stimulus was shown. Due to the partial
21 overlap with the saccade, we estimate the effective postsaccadic blanking duration to have been around 80
22 ms. Both in blanking and non-blanking conditions the postsaccadic stimulus remained on-screen for 150
23 ms, and was never followed by a mask or any other visual stimulation. Within 2000 ms after the offset of
24 the postsaccadic stimulus, the subject had to press the left button to indicate that the stimulus had moved
25 upwards, or the right button to indicate that it had moved downwards. Aborted trials were recycled after
26 each block of 50 trials; twice-aborted trials were not recycled again, but dropped from the experiment. A
27 total of 3.4% of all trials were lost.

In total, 16 conditions were measured in each subject, 100 trials each, across typically four one-hour sessions in the DPI eye tracker. Trials were collected in blocks of 50 trials, after which subjects could rest their eyes for a little while.

PLACE FIGURE 3 AROUND HERE

2.2 Results

Figure 3 shows the average proportion of correct responses in each condition. Also shown are the logistic mixed model regressions which were fitted to these data using the lme4 package for R. This type of generalized linear model analysis accounts both for the binomial nature of the response variable (through transforming proportions to logits) and the within-subject nature of the experimental design (through modeling the random subject variability around each fixed effect). The full model consisted of a fixed intercept and seven fixed effects (Size, Form, Blank, and their two-way and three-way interactions), and a random subject variability parameter for each of these fixed terms. First, we reduced the random effects structure through sequentially removing those effects whose removal did not result in a significant drop in model fit (likelihood ratio test against a χ^2 distribution). We started with the highest order terms, and only dropped lower order terms when they were not involved in a retained higher order interaction. Re-adding any of the dropped terms to the final reduced model did not result in an improved fit. Second, we reduced the fixed effect structure in a similar manner. Third, we re-added those removed random effects for which the fixed effects were retained, to maximally account for subject variability in the hypothesis testing. This was the final model:

$$\text{logit}(p) = \beta_0 + r_0 + (\beta_1 + r_1)\text{Size} + (\beta_2 + r_2)\text{Form} + (\beta_3 + r_3)\text{Blank} + (\beta_{23} + r_{23})\text{Form} \times \text{Blank} + r_{13}\text{Size} \times \text{Blank} \quad (1)$$

where p is the proportion correct, β_0 and r_0 are the fixed intercept and its random subject variability, and β_i r_i are the fixed and random regression weights for the remaining main and interaction effects, respectively.

PLACE TABLE 1 AROUND HERE

[Table 1](#) shows the fixed effect estimates, as well the standard errors of their estimation and a Wald-Z significance test. All main effects are significant, whereas the Form by Blank interaction is only marginally significant. Fixed effects that are not listed were dropped from the model during the model selection procedure and can therefore be considered highly non-significant. In a direct comparison between these beta-weights, a blank has a significantly greater effect than a form change ($\beta_3 > \beta_2$, $t(8) = 2.18$, $p = 0.03$), and the combined effect of a blank and a form change does not result in a significantly better performance than is measured with the blank alone ($\beta_3 > -\beta_{23}$, $t(10) = 0.73$, $p = 0.75$). Summarized, an intrasaccadic form change facilitated displacement discrimination, but only around half as much as a postsaccadic blank. The present data neither allowed to reject the null hypothesis that a form change improved performance on top of a blank ($\beta_3 = -\beta_{23}$), nor that full additivity existed between both effects ($\beta_{23} = 0$).

Figure 4 shows the model fit results when each type of form change (for instance, cross to diamond) received a separate β estimate under [Model 1](#). It can be seen in the upper panel that all form changes except one (square to cross) are, like the overall estimate ($\beta_2 = 0.61$), situated in between the full blanking effect ($\beta_3 = 1.34$) and the absence of any performance improvement ($\beta = 0$). The overall variation across form changes is not significant in a one-way ANOVA on these beta estimates ($F(11,5) = 2.79$, $p = 0.13$). The lower panel shows the results for the Form x Blank interactions; though highly variable, these weights are negative for 10 out of 12 form change types, which is significantly more than could be expected if these values were in reality centered around 0 (full additivity; Yates-corrected $\chi^2_{(df=1)} = 4.08$, $p = 0.04$).

PLACE FIGURE 4 AROUND HERE

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Figure 5 demonstrates the interdependence of the estimated beta weights for Form, Blank and Form x Blank across subjects. These values were obtained by applying the fixed effect part of model (1) as a separate logistic regression to each subject's data. In the left panel, the size of the form change effect can be seen to be strongly correlated with the size of the blanking effect across subjects ($\rho = 0.90$, slope = 0.40). The right panel shows the relation between the form change effect and its interaction with the blanking effect ($\rho = -0.75$, slope = -0.44). Thus, while the absolute beta values may vary considerably, their relative values are consistent across subjects.

PLACE FIGURE 5 AROUND HERE

2.3 Discussion

Referring back to the four initial questions, the following findings were critical.

First, the blanking effect of Deubel et al. (1996) is replicated in the present study. After a postsaccadic blank, intrasaccadic displacements of the saccade target object were discriminated between with a higher average accuracy than in conditions without blanking.

Second, a clear effect of form change is present, as manifested in improved displacement discrimination performance on trials where an intrasaccadic form change was applied, when compared to non-blanked conditions without such a form change. This suggests that discontinuous stimulus properties pertaining to its visual form can reject an assumption of visual stability relating to its position, and disrupt the transsaccadic stabilization process. A more veridical representation of the presaccadic stimulus position then becomes available for solving the task, probably based on extra-retinal signals. While this representation might still be perturbed by imperfect compensation for the retinal image shift, in the present experimental task it clearly does allow for a more accurate displacement discrimination performance.

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3 Importantly, the form changes used were qualitative in nature, and had a clear, common center relative to
4 which displacements were identifiable between different stimuli; if these conditions are not met, we
5 suspect the form change effect could be absent because a smaller form change would not signal a
6 disruption of visual stability, or could be severely diminished or even reversed because a form change
7 could act as a noise factor on the attribution of a given stimulus to a single spatial coordinate.
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10 Third, the results indicate that a form change was less effective in improving performance than a blank.
11 One possible explanation could be that across different types of form changes (for instance, square-to-
12 circle versus square-to-diamond) an averaging occurs of form change effects that are absent, and other
13 form change effects that are equal to the full blanking effect. Figure 4 and the analysis associated with it
14 show that this is not the case, however. No significant variation across form changes was present, and all
15 except one of the separate beta values are estimated to be at an intermediate value close to the overall
16 average effect of a form change. A similar argument might be made for individual subjects, where some
17 subjects might show a form change effect equal to the blanking effect whereas others show none. Figure 5
18 instead paints a rather different picture: The form change effect is a relatively consistent proportion of the
19 blanking effect within each individual subject. Thus, we conclude that there is in the present data an
20 overall intermediate effect of a form change compared to a postsaccadic blank. This implies that at least
21 the type of form changes we used result in a weaker facilitative effect than could theoretically have been
22 achieved on the basis of the spatial representation present in transsaccadic memory, as evidenced by the
23 superior performance of blanking conditions.
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26 Fourth, even though the simultaneous presence of postsaccadic target blanking and a form change to the
27 saccade target object diminishes the sum of their effects by about two thirds of the form change effect, the
28 formal statistical rejection of the additivity hypothesis ($\beta_{23} < 0$) was not significant. Only a weaker version
29 of this hypothesis rejection - more than half of the individual β_{23} estimates for different form change types
30 are negative - could be demonstrated to be present. The high performance induced by the blanking effect
31 alone makes it difficult to obtain reliable statistical estimates for the interaction effect. In addition, it is
32 unclear whether the improvement expected from a full additivity hypothesis could ever have been
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3 achieved. Possibly the precision of the transsaccadic positional representation limits the maximal
4 discrimination performance for a given displacement size.
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10 In the next experiment, we will address this issue by studying the interaction between postsaccadic
11 blanking duration and the presence of a form change. It is known from previous studies (Deubel et al.,
12 [1996](#)) that the blanking effect occurs for blanking durations as short as 50 ms, but does not reach its
13 maximal potential for improving performance until around 250 ms. Thus, the combined effect of a form
14 change and a shorter blank can be compared against the potential for improvement as observed using a
15 longer blanking duration. In addition, we will measure how well subjects could detect the presence of the
16 form changes, blanks and displacements employed in this experiment. This should provide explicit
17 support to what we have up to now assumed to be true, namely that form changes and blanks were easily
18 noticed by subjects, whereas failing to discriminate between displacement directions in absence of either
19 of these manipulations was underlied by subjects having perceived an unmoving stimulus.
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36 **3. Experiment 2**

37 **3.1 Methods**

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39 Five male subjects between 26 and 37 years old participated in this experiment, of which one was the first
40 author. The apparatus was identical and the procedure similar to that of Experiment 1. However, a larger
41 saccade size of 8° was used, and the screen was moved closer to the subject. At a distance of 60 cm, it
42 now occupied 32 by 24 visual degrees of the subject's field of view. This was done to allow finer-grained
43 displacements at the screen resolution used, and to make the task slightly more difficult. In addition, we
44 selected only two stimulus forms for this experiment, square and cross, in order to minimize irrelevant
45 potential variability in the data. In a $2 \times 2 \times 4$ factorial design, we combined the presence or absence of a
46 form change with two different displacement sizes (0.08° and 0.16°) and four blanking durations (0, 50,
47 58, 100 ms).
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3 100, and 250 ms). Around 30 ms of the blanks overlapped with the saccade itself. In total each subject
4 performed 100 trials in each of these conditions, amounting to 1600 trials across three to four one-hour
5 sessions. The median saccadic latency was 206 ms, with 95% of all latencies shorter than 302 ms. Less
6 than 1% of all trials was aborted twice due to late responses, incorrect eye movements or measurement
7 errors. These trials were not included in the analyses.
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16 After these sessions, additional change detection (rather than discrimination of the direction of the change)
17 measurements were done on the same five subjects, using the same stimulus presentation procedure. The
18 aim was to gauge to what degree subjects were aware of the different manipulations applied to the stability
19 or continuity of stimulus presentation. First, a single 100 trial block was run, without blanks but including
20 both displacement sizes, in which subjects were to detect whether a form change had been absent (left
21 breaker) or present (right breaker). Square-to-cross and cross-to-square changes were used on 50% of the
22 trials, whereas on the remaining 50% stimulus form remained stable at either a square or a cross. Second,
23 400 trials were run in which the saccade target object could either be displaced (50% of all trials, either
24 0.08° or 0.16°) or spatially stable (50% of all trials). This manipulation was factorially combined with
25 either a 0 ms (that is, no) or a 50 ms blank. Object forms did not change, and were either squares or
26 crosses. Subjects were instructed to respond whether the saccade target object had been stable (left
27 breaker) or unstable (right breaker). Both stimulus displacements and stimulus interruptions counted as an
28 instability for the purpose of this task. Subjects were explicitly made aware that only 25% of all trials
29 warranted 'stable' responses, and that ideally they should respond with the left button only in around one
30 fourth of trials. This was done to induce some conservatism in giving a 'stable' response given the clear
31 displacements and long blanks subjects had been perceiving previously. The median saccadic latency on
32 these additional measurements was 190 ms, with 95% of all latencies shorter than 273 ms. 2.6% of all
33 trials were dropped from the analysis after being aborted twice.
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55 56 57 **3.2 Results** 58 59 60

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3 Figure 6 shows the proportion of correct responses on the main task of the experiment, in which the
4 direction of displacement was to be identified, for both displacement sizes. A separate Form by Size
5 factorial mixed model logistic regression was applied for each blanking duration. The beta weights of
6 Form contributed significantly for blanking durations of 0 ms ($z = 4.01$, $p < 0.01$), 50 ms ($z = 2.09$, $p =$
7 0.04) and 100 ms ($z = 2.05$, $p = 0.04$), but not of 250 ms ($z = 1.05$, $p = 0.29$). This reflects the effects for
8 the smallest displacement size. Form interactions with a displacement size increase were significantly
9 positive for 0 ms ($z = 2.99$, $p < 0.01$), marginally positive for 50 ms ($z = 1.91$, $p = 0.06$), and significantly
10 negative for 100 ms blanking durations ($z = -2.17$, $p = 0.03$). The negative interaction effect at 250 ms
11 blanking duration was insignificant ($z = -1.4$, $p = 0.15$). A form change effect can therefore be said to exist
12 at 0 ms and 50 ms blanking duration for both displacement sizes, at 100 ms blanking duration for the
13 smallest displacement size, and not at all at 250 ms blanking duration. Note how performance saturates at
14 a much lower level for the 0.08° displacements. We conclude that the facilitative effects of form changes
15 and blanks can combine with each other up to a certain internal performance ceiling, which is dependent
16 on the displacement size.
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36 **PLACE FIGURE 6 AROUND HERE**
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40 Figure 7 shows the additional change detection data. When asked to detect a form change, subjects
41 performed at 97% correct. Similarly, even a 50 ms blank was responded to as an instability in stimulus
42 presentation in 98% of all trials when no simultaneous stimulus displacement was present, and 99% when
43 there was. Subjects used the prior information provided, namely that only one fourth of all trials during the
44 blank and displacement detection part of the experiment was in reality stable, relatively well: Only 35%
45 'stable' responses were given. However, this did not result in successful detection of either the 0.08° or
46 0.16° displacements: When pooled together with the actually stable trials to control for the false alarm
47 rate, average performances of 49.08% and 51.49% correct were reached, respectively. We conclude that
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3 while subjects could easily detect the presence of the form change and blanking manipulations, they failed
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5 to detect any instability when these manipulations were absent, regardless of the exact displacement size.
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10 **PLACE FIGURE 7 AROUND HERE**
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12 13 14 **3.3 Discussion** 15

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17 The main finding of Experiment 1 - form changes facilitate displacement discrimination performance -
18 was clearly replicated in Experiment 2. This effect remained weaker than the full blanking effect induced
19 by longer blanks, but was equally effective as a short 50 ms blank. Relating these discrimination data to
20 change detection rates, we observe that the failure to discriminate the direction of stimulus displacement
21 in conditions without a blank or form change is indeed underlied by a perception of positional stability
22 rather than positional uncertainty. That this is the case both for the smaller and the larger displacement
23 sizes agrees well with the finding that whereas blanked performances differ greatly between these
24 displacement sizes, their non-blanked discrimination performances are comparable. One striking finding is
25 that in these subjectively 'stable' trials, discrimination performance is still above chance. Possibly the
26 forced choice of the discrimination task was weakly driven by other information when no displacement
27 could be perceived, such as the initial saccade landing position against the displaced stimulus. In addition,
28 we observe that the form changes and blanks which led to the facilitative effects described were
29 themselves easily detected by all subjects. Combined with the earlier finding of sub-maximal facilitation
30 for form changes and shorter blanking durations, this brings on the inevitable conclusion that successful
31 explicit detection of an instability or discontinuity in stimulus presentation does not suffice to render an
32 optimally precise transsaccadic representation of the saccade target object position available for use in a
33 transsaccadic displacement discrimination task.
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3 For these relatively small displacements, the maximally attainable performance in the discrimination task
4 was strongly limited by the displacement size. This is easily explained as being the resultant of positional
5 noise induced by either the poor visual acuity of peripheral vision, or the mechanisms compensating the
6 retinal image shift based on a corollary discharge of the saccade motor command; both can be expected to
7 affect the discrimination of small displacements more than that of larger displacements. It is clear from the
8 data that form changes can improve performance on top of blanks up to this internal ceiling performance.
9 This renders the search for formal statistical additivity rather fruitless, since the individual effects of form
10 changes and blanks are too strong to have a predicted additive performance below the empirically
11 observed actual ceiling performance. However, both effects do combine with one another into a
12 performance level superior to each isolated effect, in both displacement size conditions. This leads to the
13 same conclusion as the previous paragraph: A simple instability detector, granting full access to a
14 maximally detailed and precise positional representation as soon as any sort of discontinuity in stimulus
15 presentation is detected at saccade landing, does not suffice to explain the data. Otherwise, performance
16 should not improve further by the presence of a form change after the presence of a blank had already
17 been detected. We will return to this in the general discussion.
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42 **4. General discussion**

43 *Object form subserves visual stability*

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45 MacKay ([1972](#)) already proposed that eye movements should be seen as questions, answered by their
46 resulting retinal information. Decades later, the scientific consensus appears to have indeed converged on
47 this intuition: Across the saccadic interruption of useful visual input, the visual system will assume that
48 previously stable objects have remained stable, unless convincing evidence to the contrary is present at
49 saccade landing. Under natural circumstances this is a reasonable assumption, as it is improbable that
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3 otherwise stable objects would displace themselves in exact synchrony with the observer's saccadic eye
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5 movements during scene exploration, and rather more likely that the visual system's extra-retinal
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7 compensation mechanisms for saccade-induced retinal image shifts are imperfect. The breakthrough
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9 finding of Deubel et al. (1996) that this null hypothesis of visual stability could be disrupted under the
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11 specific experimental condition of postsaccadic target blanking provided direct evidence for this view.
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13 The role of the corollary discharge for the stabilization of everyday vision is thereby reduced to that of a
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15 predictor of the impending postsaccadic visual input, specifying the null hypothesis to be tested by retinal
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17 information. It has long been hypothesized that certain form features of objects in the saccade landing
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19 region could be factored into these spatial updating mechanisms of transsaccadic vision (e.g., Deubel,
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21 Wolf, & Hauske, 1984; McConkie & Currie, 1996). Here, we offer the first empirical proof that this is
22
23 indeed the case: Subjects were significantly better at discriminating between displacement directions when
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25 saccade target objects changed form as well as position, implying that these form changes contributed to
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27 the abolition of an illusion of positional stability which was strongly present when these displaced objects
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29 also remained stable in their form properties.
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36 But, the current results in addition demonstrate that successful transsaccadic change detection by itself
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38 does not automatically give rise to the maximally attainable discrimination performance for a given
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40 displacement size. This is true for form changes when compared to blanks, but also for shorter blanks
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42 when compared to longer blanks, as already noted by Deubel et al. (1996). Moreover, though not formally
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44 additive, these facilitative effects do stack up to the empirically defined maximal task performance. Both
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46 of these facts argue against an explanation where any detected instability immediately renders available
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48 the maximally precise transsaccadic representation. Several explanations could be brought forward. First,
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50 successful explicit change detection might not always equal successful rejection of the visual stability null
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52 hypothesis, resulting in rejection rates well below 100% for form changes and shorter blanks, and in an
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54 additive increase in rejection rates when form changes and blanks are combined. Second, even when
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56 rejected in its most strict form, the visual stability assumption might continue to play a role as prior
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3 knowledge in determining the most likely displacement size given all other sources of information. Under
4 this hypothesis, form changes or shorter blanks retain a greater weight for the stable world assumption in
5 reaching a perceptual solution than is the case with longer blanking durations. This view agrees well with
6 Niemeier et al.'s (2003) Bayesian approach to the visual stability problem, and predicts graded apparent
7 displacement effects. Third, additional mechanisms might be involved. A prime candidate is a masking
8 effect on the contents of detailed transsaccadic memory, as proposed by De Graef and Verfaillie (2002)
9 and empirically supported by Germeys, De Graef, Van Eccelpoel, and Verfaillie (manuscript under
10 revision; see also McRae, Butler, & Popiel, 1987). The transsaccadic representation of object position and
11 form would then remain available to a greater degree of precision when more read-out time to a masking-
12 resilient memory store is provided through longer blanks, or when dissimilar form information is a less
13 efficient mask than identical form information.
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29 The less than perfect correspondence between on the one hand the explicit detection of a form change to a
30 transsaccadically present object and on the other hand the degree to which the discrimination performance
31 of the object's displacement is improved leaves the possibility open that not every easily detectable form
32 or feature change to the saccade target object will result in facilitative effects such as we observed. Indeed,
33 McConkie and Currie (1996) in their saccade target object theory already proposed that only a subset of
34 critical locating features would constitute a relevant input to the spatial stabilization mechanisms of
35 transsaccadic vision. More research will be needed before these relevant inputs can be characterized
36 exactly and exhaustively, however.
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49 *Form discontinuities and the landmark effect*

50 An interesting contrast between our present results and those of Deubel et al. (2002) can be noted. In their
51 study, the postsaccadic target blanking effect could be reverted by intrasaccadically inserting flanking
52 objects around the displaced position of a blanked saccade target object. Therefore it appears as if the
53 position of these flankers was taken as an indication of the position of the target object itself, despite the
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3 obvious form dissimilarity. That is, they served as a landmark for the saccade target object position in
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5 absence of the saccade target object itself. In the present study on the other hand we have observed that
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7 the visual system does not treat the saccade target object as loosely as its own spatial reference when it is
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9 discontinuous in its form properties.
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14 One could speculate that the form change dimension used by Deubel and his colleagues did not include
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16 any ‘critical locating features’, whereas ours did. However, a more plausible explanation is still to be
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18 found in the recent work of Higgins and Wang (2010). These authors suggest that landmark and blanking
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20 effects rely on different mechanisms altogether, based on the observation that flanking landmarks affect
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22 the veridicality of spatial representation similarly both across and within fixations, whereas the blanking
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24 effect of isolated saccade target objects is only facilitative in transsaccadic vision. Seeing how landmark
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26 effects therefore occur in the clear presence of the visual transient associated with a stimulus displacement
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28 – which is masked by the saccade itself in a classical transsaccadic paradigm – it would appear that they
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30 do not require an assumption of visual stability to be upheld at all.
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36 What is specific about the transsaccadic situation is that it involves the visual system in a leap of faith
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38 across an interruption of input, prompting it to recruit a mechanism aimed specifically at testing the
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40 validity of the assumptions made. Interestingly, failure to verify these assumptions for an isolated
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42 postsaccadic object such as we use does then not lead to a fallback on landmark mechanisms, even though
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44 they have been demonstrated to operate even in the presence of clear stimulus discontinuities. But while
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46 the isolated postsaccadic object will not serve as its *own* landmark, Deubel, Koch, and Bridgeman (2010)
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48 did recently demonstrate that a transsaccadically blanked stimulus can still serve as a landmark for a
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50 *second* stimulus with a longer postsaccadic blanking duration. We theorize that the form-inspecific
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52 landmark effect is essentially a two-step process (identify potential landmark, use it at the next stimulus
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54 onset) which does not apply to paradigms with a single postsaccadic stimulus presentation. There, only the
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56 form-specific visual stability assumption is relevant.
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Puzzling together the scene

Observers not only experience the visual world as being stable but also as being widely detailed, despite the anatomical reality that the human retina only allows high-acuity processing in a small, central part of the visual field. O'Regan (1992) argued that this seemingly wide field of view is but an illusion drawn up by the visual system, and that no detailed transsaccadic representation and no quantitative solution for its integration into postsaccadic vision is needed to explain the human perceptual experience. Since attention itself restricts what we are aware of, and attention is closely linked to saccadic eye movements, wondering about a specific part of the visual scene will automatically bring about a detailed representation retrieved from the external world itself. The blanking effect demonstrated that a far greater amount of information is retained across saccades than change detection tasks would indicate, offering evidence against the idea of such sparse transsaccadic representation.

However, O'Regan's view still has merit. It is indeed equally clear from the current as well as previous studies on the visual stability problem that transsaccadic perception cannot be equated with passively combining snapshots of the visual input, but that it is actively involved in constructing illusions optimized for natural situations. We would argue that transsaccadic perception of object form and features can be seen in a similar light. The fact that far more visual detail is retained across saccadic eye movements than is evident from classical change detection tasks (Demeyer et al., 2010; Deubel et al., 2002; Germeys et al. [manuscript under revision](#)) does not imply that a master scene representation of photograph-like qualities is being filled with local visual detail as foveal vision collects it across successive fixations. What it does allow is for detailed perceptual solutions reached during the previous fixation to remain relevant for postsaccadic processing down to the level of detailed visual form (Demeyer et al., 2009, 2010; Melcher, 2005), and thus provide processing speed benefits as well as transsaccadic representational continuity. The illusion of a widely detailed scene representation, richly populated with stable and unified transsaccadic

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3 object representations, is then the resultant of both the tunnel vision imposed by spatial attention and the
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5 carry-over of information on detailed perceptual solutions into the next fixation(s).
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8 9 10 *Conclusions*

11 We empirically confirm that the human visual system employs the saccade target object form to ensure a
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13 perceptual experience of visual stability, and that this process is disrupted when object form is
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15 discontinuous across the saccade. A more veridical perception of artificially applied intrasaccadic
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17 displacements then ensues. Thus, a rejection of the visual system's assumption of stability generalizes
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19 from object form to object position. The exact mechanisms involved in reaching a transsaccadic spatial
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21 representation when stability is rejected, as well as the exact set of object features underlying the saccade
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23 target object re-localization process remain fascinating topics for future research.
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60

Bridgeman, B., Hendry, D., & Stark, L. (1975). Failure to detect displacement of the visual world during saccadic eye movements. *Vision Research*, *15*, 719–722.

Bridgeman, B., Van der Heijden, A. H. C., & Velichkovsky, B. M. (1994). A theory of visual stability across saccadic eye movements. *Behavioral and Brain Sciences*, *17*, 247–292.

Cavanagh, P., Hunt, A. R., Afraz, A., & Rolfs, M. (2010). Visual stability based on remapping of attention pointers. *Trends in Cognitive Sciences*, *14*, 147-153.

Crane, H. D., & Steele, C. M. (1985). Generation-V dual-Purkinje-image eyetracker. *Applied Optics*, *24*, 527-537.

De Graef, P., & Verfaillie, K. (2002). Transsaccadic memory for visual object detail. *Progress in Brain Research*, *140*, 181–196.

Demeyer, M., De Graef, P., Wagemans, J., & Verfaillie, K. (2009). Transsaccadic identification of highly similar artificial shapes. *Journal of Vision*, *9*(4:28), 1–14.

Demeyer, M., De Graef, P., Wagemans, J., & Verfaillie, K. (2010). Parametric integration of visual form across saccades. *Vision Research*. doi:10.1016/j.visres.2010.04.008.

1
2
3 Deubel, H., Bridgeman, B., & Schneider, W. X. (1998). Immediate post-saccadic information mediates
4 space constancy. *Vision Research*, 38, 3147–3159.
5
6

7
8
9 Deubel, H., Schneider, W. X., & Bridgeman, B. (1996). Postsaccadic target blanking prevents saccadic
10 suppression of image displacement. *Vision Research*, 36, 985–996.
11
12

13
14
15 Deubel, H., Schneider, W. X., & Bridgeman, B. (2002). Transsaccadic memory of position and form.
16 *Progress in Brain Research*, 140, 165–180.
17
18

19
20
21 Deubel, H., Wolf, W. & Hauske, G. (1984). The evaluation of the oculomotor error signal. In Gale, A. G.
22 & Johnson, F. (Eds), *Theoretical and applied aspects of eye movement research* (pp. 55- 62). Amsterdam:
23 North Holland.
24
25
26
27
28

29
30
31 Deubel, H., Koch, C., & Bridgeman, B. (2010). Landmarks facilitate visual space constancy across
32 saccades and during fixation. *Vision Research*, 50, 249-259.
33
34
35

36
37
38 Duhamel, J. R., Colby, C. L., & Goldberg, M. E. (1992). The updating of the representation of visual
39 space in parietal cortex by intended eye movements. *Science*, 255, 90–92.
40
41
42

43
44 Germeys, F., De Graef, P., Van Eccelpoel, C., & Verfaillie, K. The visual analog: Evidence for a pre-
45 attentive representation within and across fixations. Manuscript under revision.
46
47
48

49
50
51 Grimes, J. (1996). On the failure to detect changes in scenes across saccades. In K. Akins (Ed.),
52 *Perception* (Vol. 2, pp. 89–110). New York: Oxford University Press.
53
54
55
56
57
58
59
60

1
2
3 Gysen, V., De Graef, P., & Verfaillie, K. (2002). Detection of intrasaccadic displacements and depth
4 rotations of moving objects. *Vision Research*, 42, 379-391.
5
6

7
8
9 Henderson, J. M. (1994). Two representational systems in dynamic visual identification. *Journal of*
10 *Experimental Psychology: General*, 123, 410-426.
11
12

13
14
15 Henderson, J. M. (1997). Transsaccadic memory and integration during real-world object identification.
16 *Psychological Science*, 8, 51-55.
17
18

19
20
21 Henderson, J. M., & Hollingworth, A. (2003). Eye movements and visual memory: Detecting changes to
22 saccade targets in scenes. *Perception & Psychophysics*, 65, 58-71.
23
24
25

26
27
28 Higgins, J. S., & Wang, R. F. (2010). A landmark effect in the perceived displacement of objects. *Vision*
29 *Research*, 50, 242-248.
30
31
32

33
34
35 Honda, H. (1989). Perceptual localization of visual stimuli flashed during saccades. *Perception &*
36 *Psychophysics*, 45, 162-174.
37
38

39
40
41 Honda, H. (1991). The time courses of visual mislocalization and of extraretinal eye position signals at the
42 time of vertical saccades. *Vision Research*, 31, 1915-1921.
43
44
45

46
47
48 Irwin, D. E. (1992). Memory for position and identity across eye movements. *Journal of Experimental*
49 *Psychology: Learning, Memory, and Cognition*, 18, 307-317.
50
51
52

53
54
55 Irwin, D. E., & Yeomans, J. M. (1986). Sensory registration and informational persistence. *Journal of*
56 *Experimental Psychology: Human Perception and Performance*, 12, 343-360.
57
58
59

1
2
3
4
5 Koch, C., & Deubel, H. (2007). How postsaccadic visual structure affects the detection of intrasaccadic
6 target displacements. In R. P. G. Van Gompel, M. F. Fischer, W. S. Murray, & R. L. Hill (Eds.), *Eye*
7 *movements: A window on mind and brain* (pp. 193–212). Oxford: Elsevier.
8
9

10
11
12
13
14 Lappe, M., Awater, H., & Krekelberg, B. (2000). Postsaccadic visual references generate presaccadic
15 compression of space. *Nature*, *403*, 892–895.
16
17

18
19
20
21 Li, W. X., & Matin, L. (1990). The influence of saccade length on the saccadic suppression of
22 displacement detection. *Perception & Psychophysics*, *48*, 453–458.
23
24

25
26
27 MacKay, D. M. (1972). Voluntary eye movements as questions. *Bibliotheca Ophthalmologica*, *82*, 369-
28 376.
29
30

31
32
33 Mathôt, S., & Theeuwes, J. (2010). Evidence for the predictive remapping of visual attention.
34 *Experimental Brain Research*, *200*, 117-122.
35
36

37
38
39
40 Matin, L., Picoult, E., Stevens, J. K., Edwards, M. W., Young, D., & MacArthur, R. (1982).
41 Oculoparalytic illusion: visual-field dependent spatial mislocalizations by humans partially paralyzed with
42 curare. *Science*, *216*, 198–201.
43
44
45

46
47
48
49 McConkie, G. W., & Currie, C. B. (1996). Visual stability across saccades while viewing complex
50 pictures. *Journal of Experimental Psychology: Human Perception and Performance*, *22*, 563–581.
51
52

53
54
55
56 McRae, K., Butler, B. E., & Popiel, S. J. (1987). Spatiotopic and retinotopic components of iconic
57 memory. *Psychological Research*, *49*, 221–227.
58
59

1
2
3
4
5 Melcher, D. (2005). Spatiotopic transfer of visual-form adaptation across saccadic eye movements.
6
7
8 *Current Biology*, 15, 1745–1748.
9

10
11 Melcher, D. (2007). Predictive remapping of visual features precedes saccadic eye movements. *Nature*
12
13
14 *Neuroscience*, 10, 903–907.
15

16
17
18 Merriam, E. P., Genovese, C. R., & Colby, C. L. (2003). Spatial updating in human parietal cortex.
19
20
21 *Neuron*, 39, 361–373.
22

23
24
25 Merriam, E. P., Genovese, C. R., & Colby, C. L. (2007). Remapping in human visual cortex. *Journal of*
26
27
28 *Neurophysiology*, 97, 1738–1755.
29

30
31 Mitroff, S. R., Simons, D. J., & Levin, D. T. (2004). Nothing compares 2 views: Change blindness can
32
33
34 occur despite preserved access to the changed information. *Perception & Psychophysics*, 66, 1268–1281.
35

36
37
38 Nakamura, K., & Colby, C. L. (2002). Updating of the visual representation in monkey striate and
39
40
41 extrastriate cortex during saccades. *Proceedings of the National Academy of Sciences of the United States*
42
43
44 *of America*, 99, 4026–4031.
45

46
47 Niemeier, M., Crawford, J. D., & Tweed, D. B. (2003). Optimal transsaccadic integration explains
48
49
50 distorted spatial perception. *Nature*, 422, 76–80.
51

52
53 O'Regan, J. K. (1992). Solving the "real" mysteries of visual perception: The world as an outside
54
55
56 memory. *Canadian Journal of Psychology*, 46, 461–488.
57
58
59
60

1
2
3 Parks, N.A., & Corballis, P.M. (2008). Electrophysiological correlates of presaccadic remapping in
4
5 humans. *Psychophysiology*, *45*, 776-783.
6
7

8
9
10 Pollatsek, A., & Rayner, K. (2002). Simple rotary motion is integrated across fixations. *Perception &*
11
12 *Psychophysics*, *64*, 1120-1129.
13
14

15
16 Pollatsek, A., Rayner, K., & Collins, W. E. (1984). Integrating pictorial information across eye
17
18 movements. *Journal of Experimental Psychology: General*, *113*, 426-442.
19
20

21
22 Pollatsek, A., Rayner, K., & Henderson, J. M. (1990). Role of spatial location in integration of pictorial
23
24 information across saccades. *Journal of Experimental Psychology: Human Perception and Performance*,
25
26 *16*, 199-210.
27
28

29
30
31 Prablanc, C., & Martin, O. (1992). Automatic control during hand reaching at undetected twodimensional
32
33 target displacements. *Journal of Neurophysiology*, *67*, 455-469.
34
35

36
37
38 Rayner, K., McConkie, G. W., & Zola, D. (1980). Integrating information across eye movements.
39
40 *Cognitive Psychology*, *12*, 206-226.
41
42

43
44
45 Ross, J., Morrone, M. C., & Burr, D. C. (1997). Compression of visual space before saccades. *Nature*,
46
47 *386*, 598-601.
48
49

50
51 Sommer, M. A., & Wurtz, R. H. (2008). Brain circuits for the internal monitoring of movements. *Annual*
52
53 *Review of Neuroscience*, *31*, 317-338.
54
55

1
2
3 Sperry, R.W. (1950). Neural basis of the spontaneous optokinetic response produced by visual inversion.
4
5 *Journal of Comparative and Physiological Psychology*, 43, 482–489.
6
7

8
9
10 Umeno, M.M., & Golberg, M.E. (1997). Spatial processing in the monkey frontal eye field. I. Predictive
11
12 visual responses *Journal of Neurophysiology*, 78, 1373-1383.
13
14

15
16 Verfaillie, K. (1997). Transsaccadic memory for the egocentric and allocentric position of a biological
17
18 motion walker. *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 23, 739–760.
19
20

21
22 Verfaillie, K., & De Graef, P. (2000). Transsaccadic memory for position and orientation of saccade
23
24 source and target. *Journal of Experimental Psychology: Human Perception and Performance*, 26, 1243–
25
26 1259.
27
28

29
30
31 Verfaillie, K., De Troy, A., & Van Rensbergen, J. (1994). Transsaccadic integration of biological motion.
32
33 *Journal of Experimental Psychology: Learning, Memory, and Cognition*, 17, 649–670.
34
35

36
37
38 von Helmholtz, H. L. F. (1866). *Handbuch der Physiologischen Optik*. Hamburg: Verlag von Leopold
39
40 Voss.
41
42

43
44 von Holst, E., & Mittelstaedt, H. (1950). Das Refferenzprinzip. *Naturwissenschaften*, 37, 464–476.
45
46

47
48
49 Walker, M.F., Fitzgibbon, E.J., Goldberg, M.E. (1995). Neurons in the monkey superior colliculus predict
50
51 the visual result of impending saccadic eye movements. *Journal of Neurophysiology*, 73, 1988-2003.
52
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For Peer Review

Tables

Effect	Weight	Estimate	SE	p(z)
	β_0	-0.405	0.137	
Size	β_1	1.140	0.095	<0.001
Form	β_2	0.611	0.157	<0.001
Blank	β_3	1.340	0.293	<0.001
Form x Blank	β_{23}	-0.403	0.239	=0.092

Table 1. Fixed regression weights and significance levels of the logistic regression model on the proportion correct data.

Figure captions

Figure 1. The four different stimuli used in Experiment 1, referred to as 'diamond', 'square', 'circle', and 'cross'.

Figure 2. Subjects started each trial by fixating a cross on the left of the screen. After a random delay, a stimulus appeared to the right, to which they were instructed to saccade as quickly as possible. The vertical position of the stimulus always changed during the eye movement, and on half the trials the stimulus form was altered as well. The postsaccadic stimulus was either immediately present or preceded by a brief blank screen (on half the trials). The task was to ignore form changes, and judge the direction of displacement as being upward or downward.

Figure 3. Proportion correct results for all subjects. Symbols represent data points averaged across subjects, with error bars indicating one standard error of between-subject variability. Blue and green lines represent the logistic regression model fit to these data points (see [Table 1](#)); the orange line illustrates the theoretical prediction of an additive combination of the isolated form change and blank effects. Main effects of displacement size, form change and blanking are clearly present, but the departure from additivity (full green line vs. dotted orange line) is not statistically significant.

Figure 4. a) Estimated beta-values for each type of form change, in absence of blanking. Analogous to Figure 3, the interrupted blue line indicates the baseline performance in absence of a form change, the

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3 interrupted green line indicates the average form change effect, and the full blue line indicates the average
4 blanking effect. All but one form change type result in an intermediate performance level, lending support
5 to the notion of an overall intermediate effect of these form changes. b) Similarly, estimated beta-values
6 for the Form x Blank interaction. The dotted orange line illustrates the additivity hypothesis, the full blue
7 line a performance level equal to that of the isolated blanking effect alone. The full green line indicates the
8 average Form x Blank effect. It can be seen that although the overall Form x Blank effect is not
9 significant, all but two beta-weights are negative. The error bars in both figures denote one standard error
10 of estimation.
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25 **Figure 5.** a) The estimated Form and Blank beta weights for individual subjects. Analogous to Figure 3,
26 the interrupted blue line illustrates the absence of a form change effect, the full blue line illustrates a form
27 change effect equal to the blanking effect. The interrupted green line is a linear fit on these individual
28 subject data, whereas the triangle indicates the estimated average Form and Blank effects of Table 1. The
29 form change effect can be described as a relatively fixed proportion of the blanking effect across subjects.
30 b) The relation between the Form and Form x Blank beta weights across subjects. The dotted orange line
31 indicates the additivity hypothesis, the full blue line is equal to the absence of any form change effect on
32 top of the blanking effect. The full green line is a linear fit to the estimated individual beta weights,
33 whereas the triangle again indicates the estimated average beta weights of Table 1. All subjects but one
34 are compatible with a strongly negative relation between the Form and Form x Blank effects. Error bars in
35 both figures indicate one standard error of estimation.
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53 **Figure 6.** Proportion correct results for Experiment 2, subdivided by blanking duration. The colors and
54 symbols have no relation to those of the previous figures. In absence of a blank, a form change greatly
55 improves performance. Longer blanking durations lead to less improvement, up to an internal ceiling
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3 performance dependent on the displacement size applied. Error bars indicate one standard error of
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5 between-subject variability for each data point.
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11 **Figure 7.** Additional change detection results for Experiment 2. The colors have no relation to those of the
12 previous figures. Form changes and 50 ms blanks were almost always correctly detected, whereas
13 displacements in absence of either of these manipulations could not be distinguished from non-displaced
14 trials, independent of the exact displacement size. Error bars denote one standard error of between-subject
15 variability.
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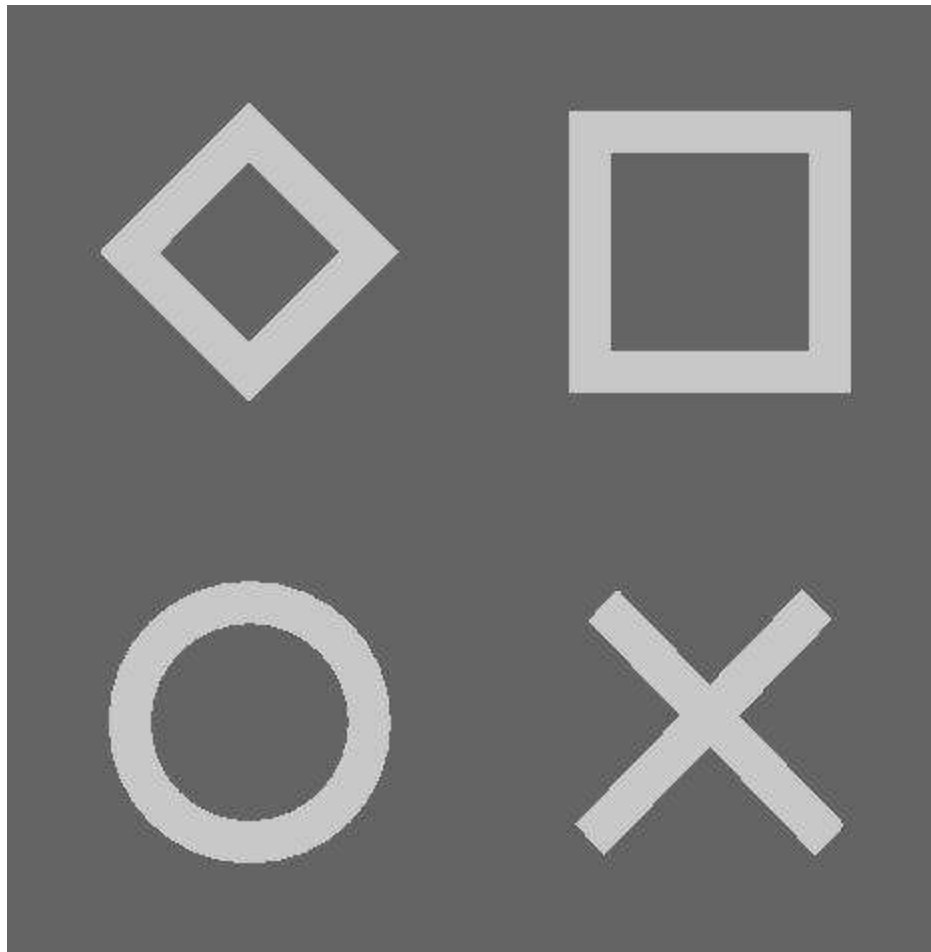


Figure 1. The four different stimuli used in Experiment 1, referred to as 'diamond', 'square', 'circle', and 'cross'.
19x20mm (600 x 600 DPI)



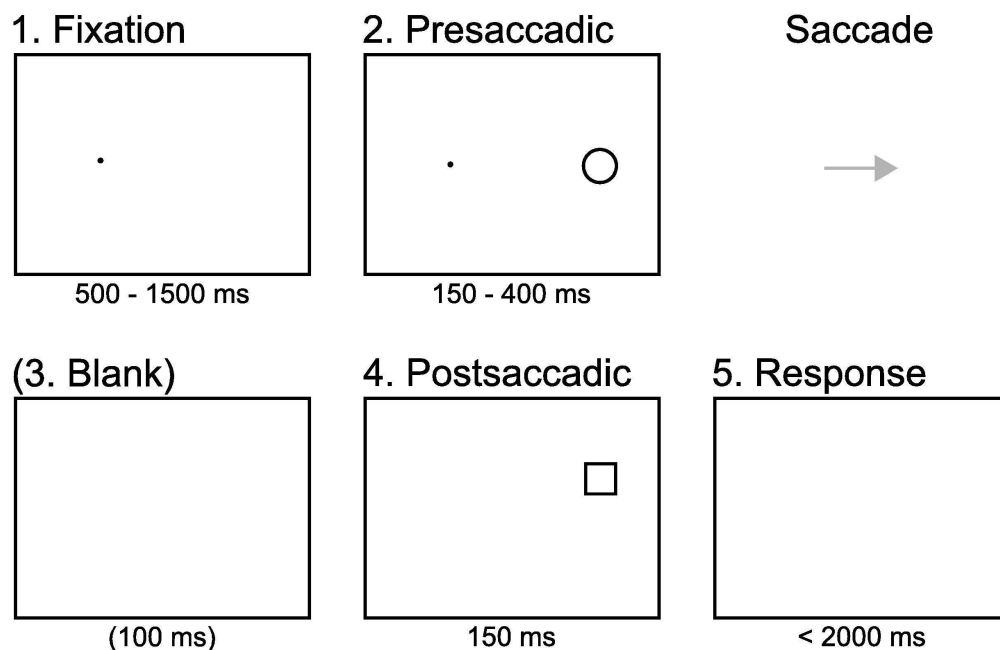


Figure 2. Subjects started each trial by fixating a cross on the left of the screen. After a random delay, a stimulus appeared to the right, to which they were instructed to saccade as quickly as possible. The vertical position of the stimulus always changed during the eye movement, and on half the trials the stimulus form was altered as well. The postsaccadic stimulus was either immediately present or preceded by a brief blank screen (on half the trials). The task was to ignore form changes, and judge the direction of displacement as being upward or downward.
103x66mm (600 x 600 DPI)

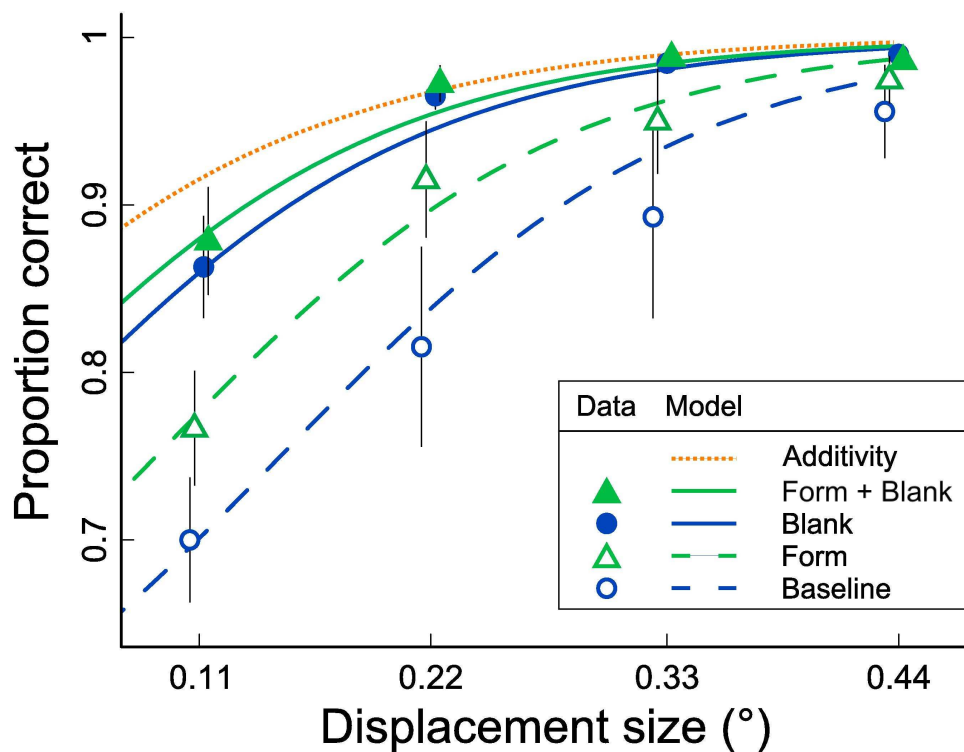


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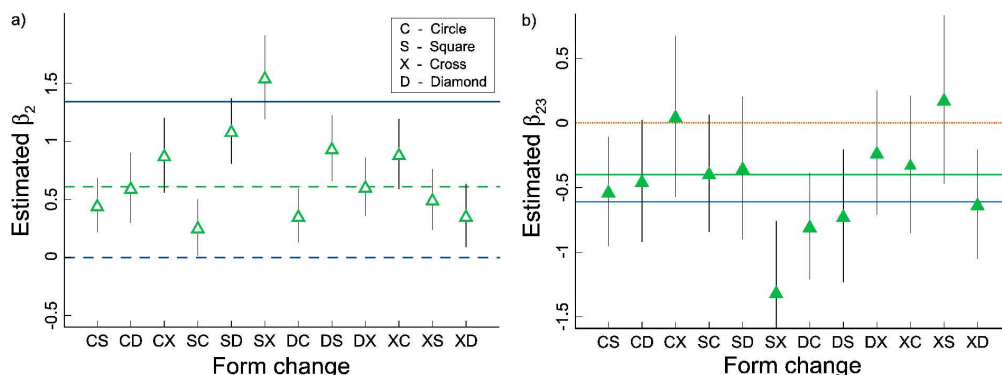


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240x88mm (600 x 600 DPI)

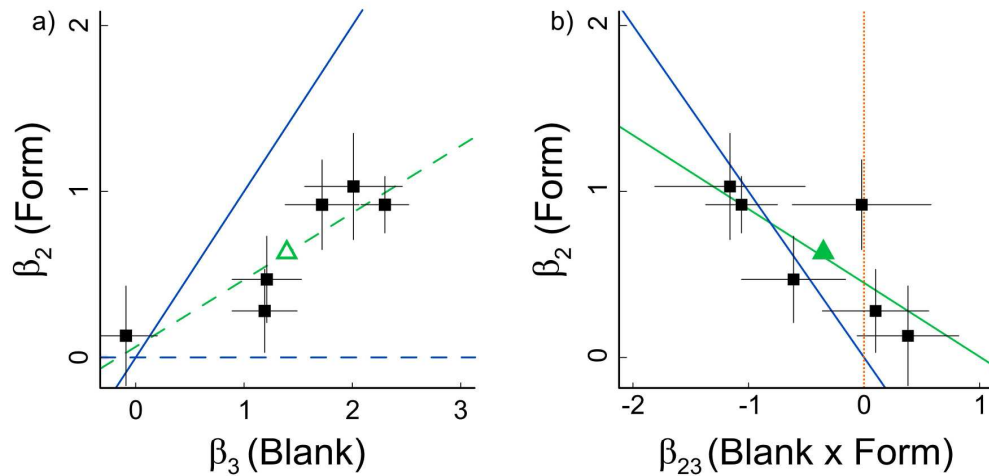


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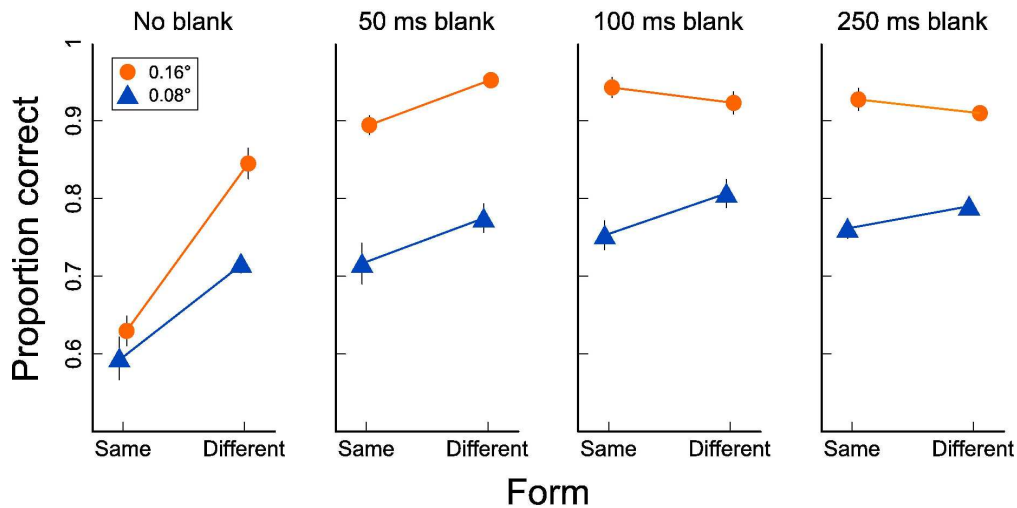


Figure 6. Proportion correct results for Experiment 2, subdivided by blanking duration. The colors and symbols have no relation to those of the previous figures. In absence of a blank, a form change greatly improves performance. Longer blanking durations lead to less improvement, up to an internal ceiling performance dependent on the displacement size applied. Error bars indicate one standard error of between-subject variability for each data point.

156x77mm (600 x 600 DPI)

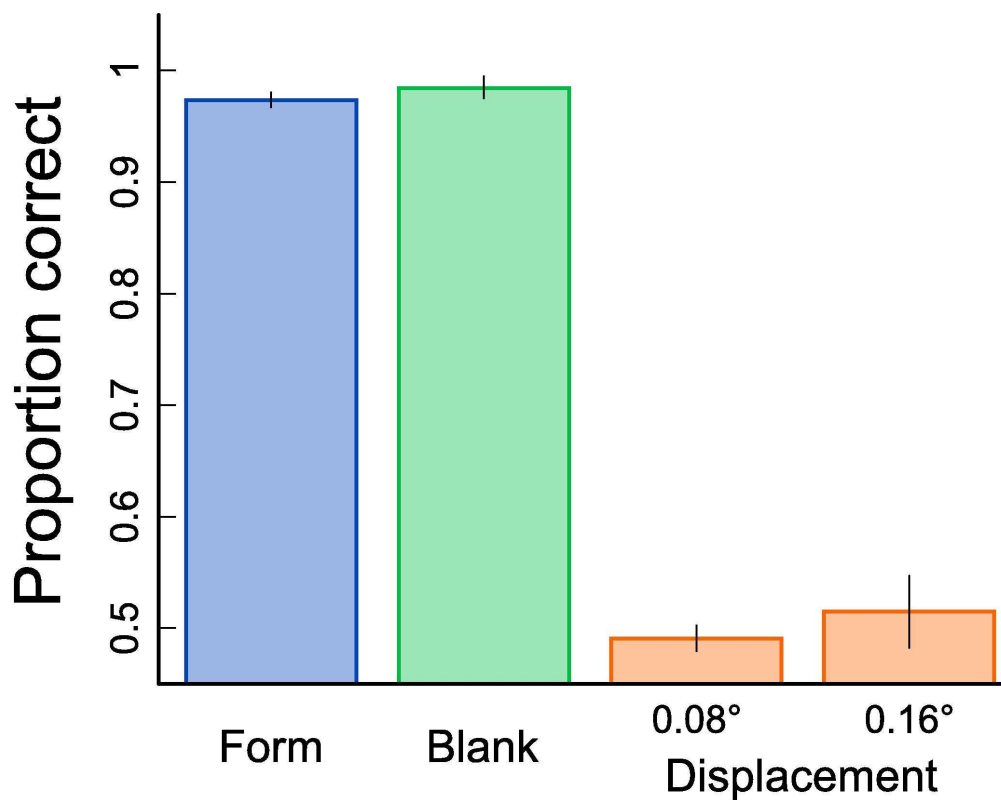


Figure 7. Additional change detection results for Experiment 2. The colors have no relation to those of the previous figures. Form changes and 50 ms blanks were almost always correctly detected, whereas displacements in absence of either of these manipulations could not be distinguished from non-displaced trials, independent of the exact displacement size. Error bars denote one standard error of between-subject variability.

87x69mm (600 x 600 DPI)