Motion-induced scotoma

Tatjana Seizova-Cajic[1], Nika Adamian[2,3], Marianne Duyck[3,4], Patrick Cavanagh[3,5,6]

[1] Touch, Proprioception and Vision Laboratory, Faculty of Health Sciences, University of Sydney, Sydney, 2141 NSW, Australia

[2] School of Psychology, University of Aberdeen, AB24 3FX, Old Aberdeen, UK

[3] Laboratoire Psychologie de la Perception, CNRS UMR 8242, Université Paris Descartes, 75006 Paris, France

[4] Laboratory of Sensorimotor Research, National Eye Institute and National Institute of Mental Health, National Institutes of Health, Bethesda, MD 20892, USA

[5] Department of Psychological and Brain Sciences, Dartmouth College, Hanover, NJ 03755, USA

[6] Department of Psychology, Glendon College, CVR York University, Toronto, ON M4N3M6, Canada

[1] Corresponding author (tatjana.seizova-cajic@sydney.edu.au)

Abstract

We investigated artificial scotomas created when a moving object instantaneously crossed a gap, jumping ahead and continuing its otherwise smooth motion. Gaps of up to 5.1 degrees of visual angle, presented at 18º eccentricity, either closed completely or appeared much shorter than when the same gap was crossed by two-point apparent motion, or crossed more slowly, mimicking occlusion. Prolonged exposure to motion trajectories with a gap in most cases led to further shrinking of the gap. The same gap-shrinking effect has been observed in touch (Seizova-Cajic & Taylor, 2014). In both sensory modalities, it implicates facilitation among co-directional local motion detectors and motion neurons with receptive fields larger than the gap. Unlike stimuli that simply deprive a receptor surface of input, suggesting it is *insentient*, our motion pattern skips a section in a manner that suggests a portion of the receptor surface has been *excised* and the remaining portions stitched back together. This makes it a potentially useful tool in the experimental study of plasticity in sensory maps.

Keywords

Artificial scotoma; completion; filling-in; motion; plasticity

Moving objects may temporarily disappear from view, a common reason being occlusion by other objects. For an object moving at a constant velocity, the time for the object to reappear can be predicted from its velocity prior to occlusion (Fig. 1A, leftmost stimulus). For other velocity profiles, time of reappearance is not necessarily predictable (Fig 1A, middle and right). However, for *all* velocity profiles, the occluder affects the visibility of the moving object but not its velocity: the visible motion and the hidden motion should be similar because the occluder is merely an accidental masking of part of the object's trajectory. This independence of the occlusion and the occluded motion helps us to infer the velocity and path of the hidden trajectory and a successful prediction of the emergence of the object in turn supports the impression that there is an occluder. Natural and acquired blind spots (scotoma) also create discontinuities in the motion path registered by the sensory surface, although this discontinuity is not necessarily perceived. As with occlusion, the loss of part of the motion trajectory caused by a scotoma has no effect on the trajectory itself.

In the experiments presented here, we violated this independence between trajectory and occluder by having a trajectory with a gap, as if there were an occluder, but where the object almost *instantly* (in 8 ms) reappears at the other side of the gap (Fig. 1B *Right*). The similarity with occlusion (Fig. 1B *Left*) is that the motion trajectory is interrupted by a spatial gap, simulating a scotoma (Fig. 1C *Left*). The difference is that in our stimulus there is no corresponding temporal gap, implying an extreme velocity while the object is not visible. This effect of the gap on the velocity while the object is hidden makes occlusion an unlikely explanation of the gap.

A more likely possibility is a discontinuity in the sensory surface itself. Specifically, our stimulation pattern (labelled 'Abridging' by Seizova-Cajic & Taylor, 2014) would occur if an area had been excised from the receptor surface, and the previously remote parts stitched together (Fig. 1C *Right*). We assume that, with sufficient repetition, this *simulated rearrangement* of the receptor surface would likely trigger a reorganization of the higher-level representation of locations to regain continuity. It would be similar to somatosensory cortex reorganization after a real, surgical rearrangement of the receptors (Merzenich & Jenkins, 1993).

Motion of objects in the world can serve to relate different parts of the scrambled jigsaw puzzle – an undeveloped or damaged sensory map - and allow its ordering (Lotze, 1852, cited in Boring, 1950; Koenderink, 1990). This is computationally possible as a form of unsupervised learning. When felt or seen locations for each receptor are adaptable, over time, repeated exposure to objects moving smoothly in the world would give rise to an experience of continuous motion: the location-coding receptor surface would eventually be calibrated to match the continuity of trajectories in the world (Maloney & Ahumada, 1989).

The above analysis assumes object constancy i.e., that the observer perceives one and the same moving object on all parts of the motion trajectory even when the trajectory is incomplete. This assumption is consistent with a large body of literature, from Gestalt psychology to attentional tracking (see Chun, & Cavanagh, 1997; Kanai, Sheth, & Shimojo, 2007; Pessoa, Thompson, & Noë, 1998; Todorović, 2011; Wertheimer, 1923).
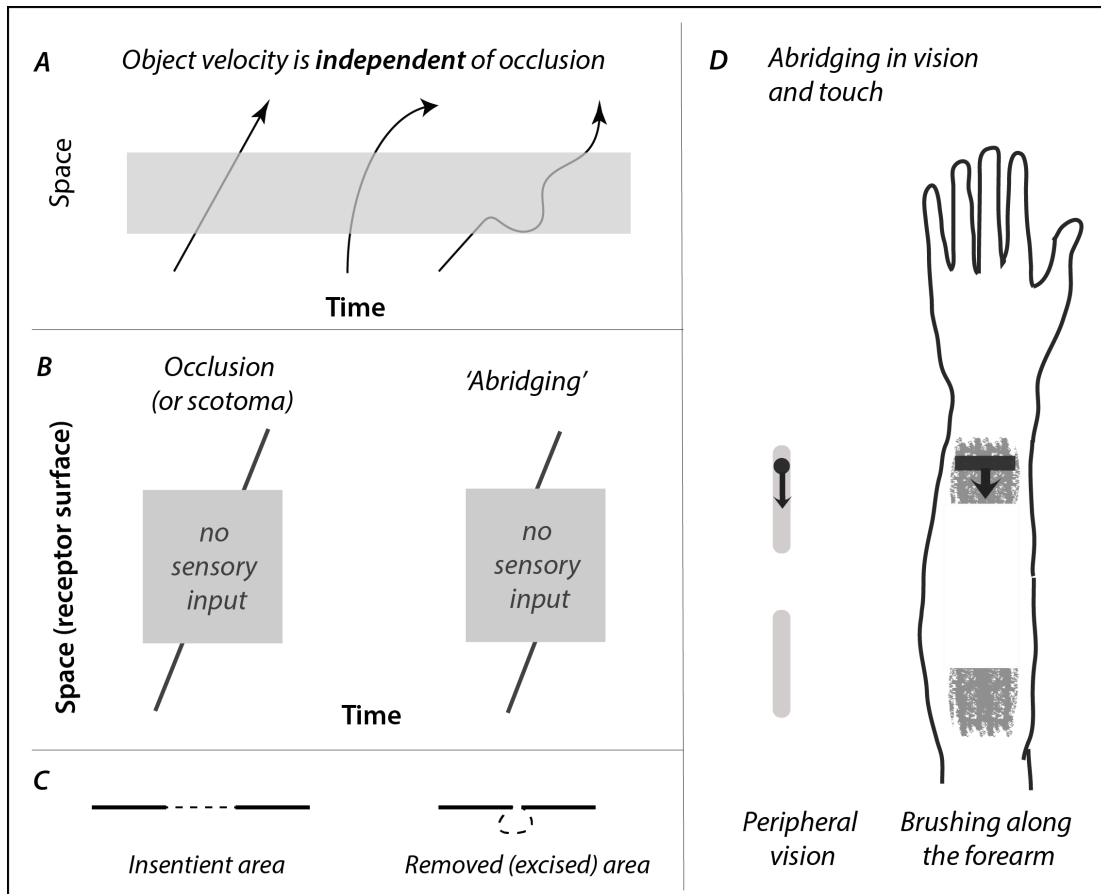
Figure 1. **A**. A time-space diagram of three different, partially occluded motion trajectories (occluders shown as semi-transparent surfaces represent complete occlusion). Note that occluder placement is not related to the motion event: velocity bears no relationship to occlusion. **B**. *Left* A time-space diagram showing an object that moves behind an occluder/across the blind spot with no change in average velocity; *Right* The 'Abridging' stimulus moves at the constant velocity along the visible parts of the trajectory but crosses the gap in an instant. **C**. Schematic illustration of receptor surfaces (represented by a line) that different motion patterns simulate: *Left* The occluded area, represented as a dashed line segment, is insentient (a scotoma in vision and numb spot in touch); *Right* The area skipped using our Abridging pattern (a dashed curve) has been removed, and the remaining edges sutured together. **D**. Spatial representations of the Abridging stimulus presented in peripheral vision (present study), and on the forearm (Seizova-Cajic & Taylor, 2014). In both cases, when the stimulus reaches the front edge of the gap, it instantaneously continues from the back edge of the gap. In the tactile case, this is accomplished by having two brushes and the second touching the skin after the gap just after the first has reached the beginning of the gap.

We expect long-term exposure to the Abridging stimulus to result in sensory reorganization – a hypothesis yet to be tested – but the question is also how it is initially perceived, i.e., how does the visual system deal with such spatio-temporal patterns? In the present study, our participants reported whether they could see the spatial gap and how large it was when the Abridging stimulus was seen in peripheral vision (Fig. 1D, *Left*).

Our stimulus here is visual but an analogous somatosensory stimulus had previously been applied to the skin of the forearm (Fig. 1D, Right). It included a 10-cm spatial gap, but most participants felt no gap – they reported an *uninterrupted motion* along the forearm instead (Seizova-Cajic & Taylor, 2014, Fig. 3; Nguyen, Taylor, Brooks & Seizova-Cajic, 2016, Fig. 2). In contrast, the gap was clearly felt, and its perceived size was approximately veridical when temporal and spatial gaps were consistent with each other, as they would be in the case of natural occlusion or scotoma.

Here we investigate the visual appearance of the Abridging stimulus. Our main finding is that peripherally (at 18° of visual angle eccentricity) presented gaps in a motion path of up to 5.1° of visual angle are partially or completely filled-in with motion (Experiment 1). Filling-in does not occur if time the stimulus takes to cross the gap is long enough to mimic the crossing behind an occluder or through a scotoma. Repeated sweeps across the gap aid the filling-in (Experiment 2).

General Methods

Perceptual effects of the Abridging stimulus were explored in two psychophysical experiments. Common features of the experiments are described first, followed by detailed description of each experiment.

Participants

All participants gave informed consent in writing prior to participation and the protocols for the study were approved by the Université Paris Descartes Review Board, CERES, in accordance with French regulations and the Declaration of Helsinki. Participants were compensated 10€ per hour for their time. They all reported normal or corrected-to-normal vision. None of the authors participated as subjects, and different participants took part in each experiment.

Procedure

The experiment took place in a dimly lit room (0.02 cd/m^2). Visual display was projected with a PROPixx projector (VPixx Technologies Inc.) at 120 Hz. Participants sat at 130 cm distance from the projection screen where the computer controlled images subtended 60 by 34 degrees of visual angle (dva). The right eye was monitored using an Eyelink 1000 Plus desktop mount (SR Research Ltd.) at 1000 Hz. A head and chin rest ensured stability of the head. Fixation was monitored throughout the trial. If a saccade, a blink, or a deviation of more than 2 dva from initial fixation was detected, the trial was aborted and readministered later in the experiment.

A practice block of 30 trials was performed at the beginning of each experiment. A message displayed on the computer screen encouraged participants to take breaks every 30-40 trials.

Stimuli

The stimulus was a disc of 0.45 dva radius. It was presented at the eccentricity of 18 dva and moved along the vertical trajectory (15 dva) at the speed of 20 dva/s. The eccentricity varied randomly within of 18 ± 2 dva in order to minimize light adaptation at a given retinal location. The trajectory had a segment in the middle within which the stimulus was not visible – a 'gap'. This spatial gap varied in size between 0.1 to 5.1 dva. The direction of the first sweep (the only sweep in some experimental conditions) was determined at random. The fixation point was 0.1 dva in radius. A rectangular probe with a gap in the middle, centred at the fixation point, appeared at the start of the trial. The initial size of the gap in the probe was between 1 and 5 dva, chosen at random. After the target disappeared from the screen, the probe became adjustable using the wheel on the computer mouse. The step size for adjustment was 0.1 dva, minimum gap size was zero and maximum size was limited only by the size of the screen (34 dva). Response time was not limited.

The lightness levels were 45 cd/m^2 for the background (mid-grey), 27 cd/m^2 for the stimulus (dark grey), 0.06 cd/ m^2 for the fixation point (black), and 72.9 cd/ m^2 for the probe (light grey).

Data analysis

Raw data in both experiments were gap size estimates in degrees of visual angle (dva). We analysed them in two ways described below.

The aim of the first analysis was to show the probability of filling-in in each condition, and we reduced data to **binary values**: zero gap-size responses were classified as 'filled-in', and all non-zero responses as 'not filled-in'. We used contour plots to visualize any trends and computed the probability of filling-in in different conditions using logistic regression in SPSS.

The aim of the second analysis was to determine perceived gap size in different conditions. Data were treated as **continuous** variables and analysed using Linear Mixed Model (LMM) for repeated measures data via General Linear Model (GLM) procedure in SPSS. LMM accounts for repeated nature of the data and for random variation across individuals. It also allows independent variables such as gap size to be treated as continuous measures (West, Welch & Galecki, 2015). Fixed factors were gap size and other manipulated factors (different across the two experiments), and repeated exposure to stimuli. Participants were treated as a random factor, defined in the Random subcommand in SPSS, with the specific covariance structure defined in the G matrix. This removed a significant proportion of within-subject covariance from the residuals. The Repeated subcommand with its specific R matrix dealt with the remaining within-subject correlations. Unlike the standard linear model, LMM allows the residuals from the repeated observations on the same participant to be correlated, and their specific covariance structure is defined in the R matrix. (For more details regarding G and R matrices, see section 2.2.2, West et al, 2015).

Details that varied across experiments are described in the relevant sections. LMM relies on maximum likelihood (ML) for parameter estimation, and we evaluated our models using -2LL and AIC information criteria. Restricted ML (REML) was used to estimate random effects and final model fit, and ML for estimation of fixed effects.

Experiment 1: Motion induced filling-in

The critical manipulation in this experiment concerned the Motion context i.e., the motion of the visual target before and after crossing of the gap. In the *Abridging* condition, the target moved continuously up-and-down along the eccentrically presented vertical 15 dva path, with a variable gap in the middle of the path. As soon as it reached one side of the gap and disappeared, it reappeared on the other side. In the control, *Jump* condition, the target dot did not move before or after crossing the gap: it appeared at a single position adjacent to the gap, disappeared and reappeared on the opposite side. It remained there for the same amount of time before 'jumping' again.

The additional control condition, *Occlusion* (completed by two participants only), was identical to Abridging, except for the gap-crossing time. It mimics occlusion or scotoma (see Fig. 1B). Time-space diagrams of all three stimulus types are shown in Figure 2, and video demonstrations are available online (Animations 1 – 3).
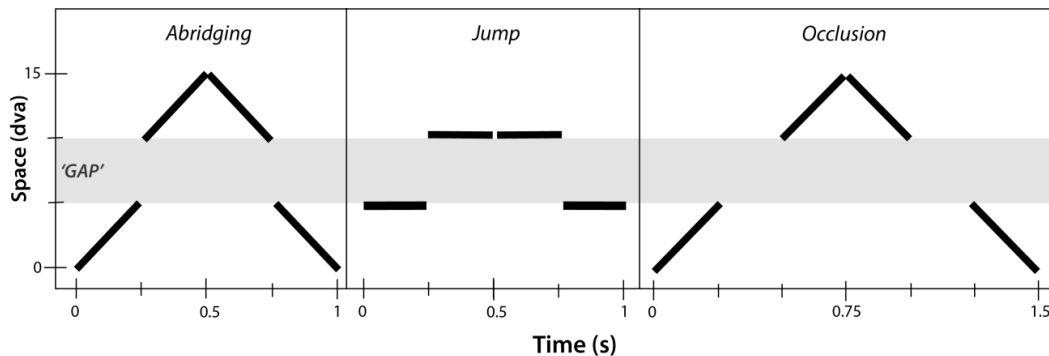
Figure 2. Time-space diagrams of single cycle of the stimuli used in Experiment 1. Eight observers completed the Abridging and Jump (control) conditions in a repeated-measures design. 'Occlusion' was an additional control completed by two new observers.

Method

Main experiment: Eight participants (4 males), aged 18-43 (M=27.5), observed the motion and used the mouse wheel to adjust the gap size in the centrally presented probe to match the perceived gap size in the motion trajectory. The probe was on the screen throughout the trial but only became adjustable after 3, 4 or 5 motion sweeps (one 'sweep' = motion in one direction, upward or downward) i.e., after 3, 4 or 5 target jumps across the gap.

Temporal aspects of the stimulation were matched in the Abridging and Jump conditions: duration of each half-sweep in the Abridging condition was equal to the presentation time of the dot on either side of the gap in the Jump condition, and gap-crossing times were equal and nearly instantaneous (duration of one frame i.e., 8.3 ms). The Occlusion condition was identical to Abridging, except for the gap-crossing time, which varied with gap size, consistent with constant target velocity during 'occlusion'.

The eleven gap sizes used ranged from 0.1 to 5.1 dva (0.1, 0.8, 1.1, 1.8, 2.1, 2.8, 3.1, 3.8, 4.1, 4.8 and 5.1 dva). The speed of dot motion in the Abridging condition was 20 dva/s, and total trajectory length (including the variable gap) was 15 dva. Because of the varying gap sizes, dot presentation time in each direction of motion was also variable: for minimal gap size it was approximately 714 ms (86 frames x 8.3ms), and for maximal gap size 465 ms (56 frames x 8.3 ms). All stimuli were presented in peripheral vision, to the left or right side of the fixation point, chosen at random in every trial.

Each participant completed a total of 440 trials (2 motion context conditions x 11 gap sizes x 20 repeats), equally split across two sessions and presented in random order within each session. Presentation side (left vs. right) and number of sweeps (3, 4 or 5) were randomly chosen in each trial and did not necessarily have equal number within each of the main conditions. They were not treated as factors in the data analysis.

Additional control: Two new participants (males aged 25 and 32) completed the Abridging condition from the main experiment, and the new, *Occlusion* control condition identical in all respects except for the gap-crossing time. This was nearly instantaneous for the Abridging case, but was the time it should take if the target moved at constant velocity while not visible in the Occlusion condition. This control mimics a real occlusion.

Data analysis

We conducted two separate analyses, as described in the General Methods section: one treated the data as binary, and the other, as continuous. Each participant contributed 440 data points to each analysis, 10 for each of the 44 unique conditions defined by crossing of 2 Motion contexts (Abridging, Jump), 11 Gap sizes and 2 Sessions. Our main interest in both analyses was in the effect of Motion context.

Analysis 1, binary data: We computed the probability of filling-in as a function of Motion context and Gap size. Group results were plotted to show trends across conditions and time. Individual results were subject to the logistic regression in SPSS to determine equal-probability threshold for gap detection (gap size equally likely to be seen or filled-in).

Individual equal-probability thresholds for seeing the gap were computed separately for the two Motion contexts. There was rarely any filling-in for gap sizes greater than 2.1 dva in the Jump condition (as shown in Fig. 3, top left panels), and only the smallest five gap sizes were used to determine the threshold (0.1 – 2.1 dva). By contrast, all eleven gap sizes were used in the Abridging condition. The number of

stimuli per participant was therefore 100 in the Jump condition (5 Gap Sizes x 20 repeats) and 220 in the Abridging condition (11 Gap Sizes x 20 repeats). Session (1st, 2nd) was included as a factor in the preliminary analysis. The gap-detection threshold was higher in the second session for most participants, but the effect was not significant, except for one participant in one condition.

Analysis 2, gap size estimates: The dependent variable here was Perceived gap size in degrees of visual angle. We were interested in the effects of Motion context, Gap size, Session, and exposure within each session, labelled 'Repeats' (exposure was operationalized as the order of repeated presentations of the same stimulus within each session; each stimulus was presented 10 times, and since conditions were randomized, repeats were usually, but not necessarily always, sequential; e.g., repeat #6 for one gap size could come before repeat #4 for a different gap size). Gap size and Repeats were treated as continuous variables. The final solution in LMM analysis included fixed factors of Gap size (a continuous variable represented with 11 values), Motion context (Abridging and Jump), Session (1st, 2nd), Repeats (10 per condition), quadratic components for Gap size and Repeats, and significant interactions. Inter-subject variations in intercepts and slopes of functions relating Gap size to Perceived gap size were random factors, specified separately for each Motion context. Residual variance increased with Gap size and was also different across the two levels of Motion context: it was greater in the Abridging than Jump condition. The model accounted for this by specifying heterogenous compound symmetry (CSH) for the R matrix structure.

Data from the two participants who completed the additional control condition in Experiment 1 were plotted with 95% CI for visual inspection.

Results

Binary data

Motion context dramatically affected the probability of seeing the gap: gaps were usually visible in the Jump condition (black areas in contour plots, Fig. 3), but were usually *not* seen in the Abridging condition (red, white and grey areas in contour plots, Fig. 3). The filling-in occurred with greater frequency in the 2nd than in the 1st Session and was also more common as the sessions progressed than in the first two presentations, with both trends more visible in the Abridging than in the Jump condition.

Out of 8 participants, four nearly always reported the gap in the Jump condition (in 98-100% of trials), and one nearly always reported no gap in the Abridging condition (in 99% of trials); gap detection thresholds for them could not be calculated using logistic regression. They could also not be calculated for one participant who did not hit floor or ceiling. For the remaining participants and conditions, the logistic regression produced a significant omnibus test of model coefficients. As shown in Fig. 3 *Right*, their thresholds are much lower in the Jump (approx. 0.5 dva) compared to Abridging condition (approx. 3.0 dva). If we assign 0.1 dva threshold to individuals with the floor effect, and 5.1 dva to those with ceiling effect, the respective group means become 0.35 dva and 3.30 dva.
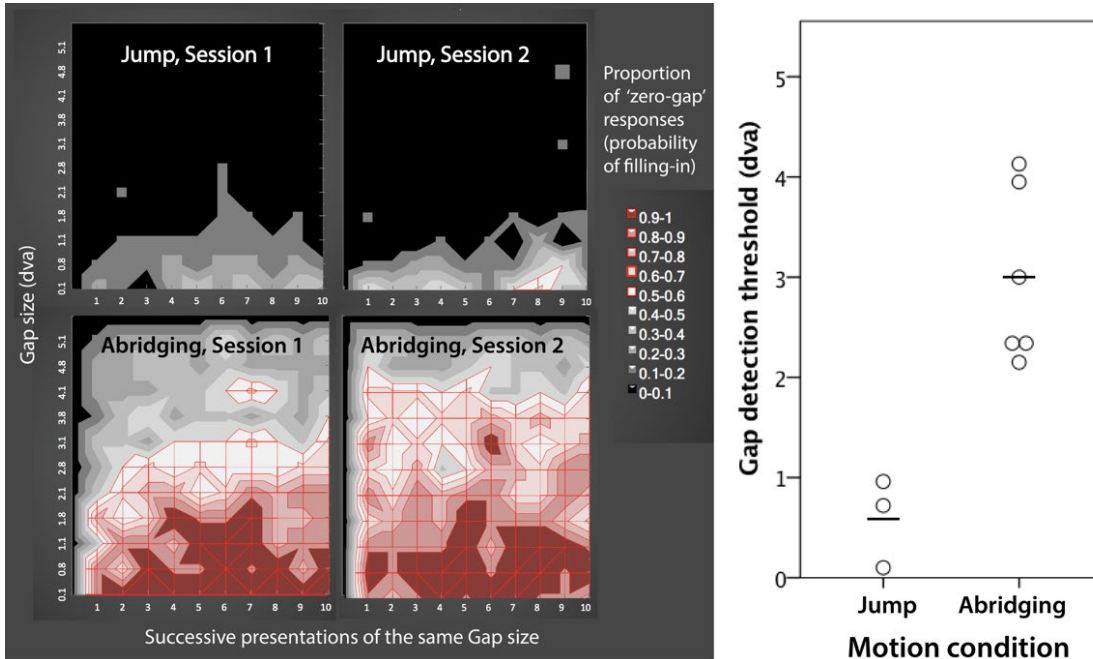
Figure 3. Results of Experiment 1, binary data (zero-gap vs non-zero gap) *Left panels:* Probability of zero-gap responses across all participants (n=8) is shown as a function of Motion context (Jump, Abridging), Gap size (y-axis), and exposure to the repeated presentations of the same Gap size within each session (x-axis) and across sessions (left and right panels). The probability is represented by colour: black areas indicate non-zero gaps (absence of filling-in), and dark red areas, mostly zero gaps (filling-in). Areas with red outline indicate proportions of 0.5 or higher of filling-in. *Right panel:* Individual equal-probability thresholds for gap detection/filling-in. Individual thresholds are represented as circles, and group means as short lines. Thresholds are only shown for participants for whom the logistic regression produced the significant omnibus test of model coefficients, 3/8 participants in the Jump condition, and 6/8 in the Sweep condition.

Gap size estimates

Gaps were perceived as far narrower in the Abridging than in the Jump condition including the largest, 5.1-dva gap, similar in size to the natural blind spot (see left and middle panels of Fig. 4).

Responses in the second session were smaller than in the first for both Motion conditions (both curves are lower in the middle than the left panel), and the last, 10th response to the same gap size within each session was smaller than the 1st response by approximately 0.3 dva, with markedly different trends across gap sizes for the two conditions (rightmost panel).

The LMM analysis revealed a significant effect of Gap size ($F_{(1, 7.1)} = 109.3$, $p < .001$), Motion context ($F_{(1, 397)} = 410.3$, $p < .001$), Session ($F_{(1, 365)} = 13.4$, $p < .001$) and Repeats ($F_{(1, 343)} = 4.3$, $p < .039$). Quadratic trend for Gap size was also significant ($F_{(1, 2135)} = 75.4$, $p < .001$), and so were multiple interactions.
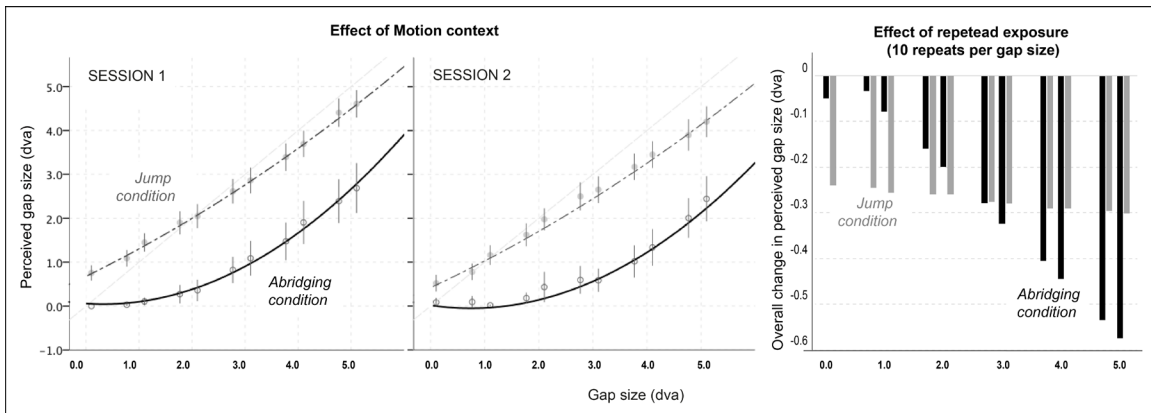
Figure 4. Perceived gap size, Experiment 1 (n=8). *Left and middle panel:* Reported gap size as a function of physical gap size (11 gap sizes were presented) and Motion context (Jump vs Abridging). Parameters of the fitted curves were estimated using linear mixed modelling procedure. Error bars are 95% CIs for the group means (these are irrelevant for the analysis, which took into account the repeated measures nature of the data). *Right panel*: Change in the perceived gap size between the 1st and 10th repeat as a function of Gap size and Motion context. Note that all values are negative, i.e., perceived size always decreased. However, the amount of decrease depended on Gap size and Motion context.

The interaction between Gap size^2 and Motion context (F(1, 1295) = 33.2, p < .001) reflects differences in curvature with increase in gap size between the two Motion conditions. The responses in the Abridging condition start from a lower base than in the Jump condition and increase more as the gap size increases (Fig 4, left or middle panels).

The 3-way interaction between Gap size, Motion context and Repeats shows that the response change to different gap sizes with their repeated presentations differs in the Jump and Abridging conditions (F(2, 828) = 5.0, p = .007). The overall response change from the beginning to the end of the session is shown in Fig. 4, right panel. It depended strongly on the Gap size in the Abridging condition (black bars), but very little in the Jump condition (grey bars).
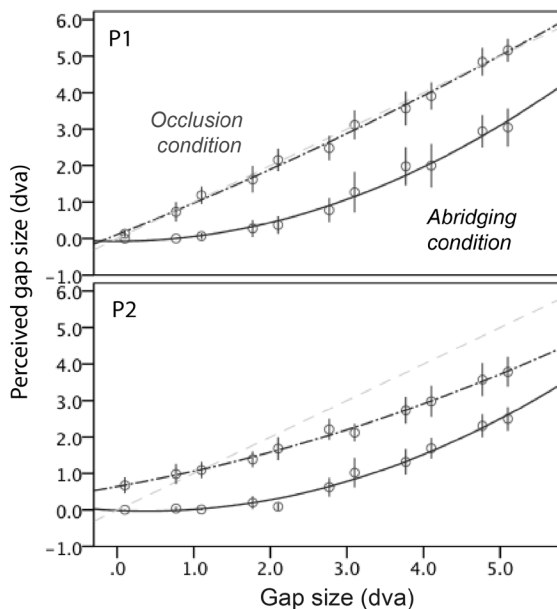
The highest order interaction included in the model tested the relationship between quadratic terms for Gap size and Motion context,

Figure 5. Perceived gap size as a function of physical Gap size and Motion context (Occlusion vs Abridging), additional control experiment. The Occlusion is a new condition (illustrated in the rightmost panel, Fig. 2). Each panel shows the results of one participant. Error bars are 95% CIs for the means, based on 20 repeats per condition.

Repeats, and Session. It was significant (F(4, 673) = 2.6, p = .034), showing that the two-way and three-way interactions described above take a slightly different form in two different sessions, and also revealing the quadratic nature of response change with repeated presentations.

Gap size estimates in the additional control experiment (n = 2) are shown in Fig. 5. The perceived gap sizes in the Occlusion and Abridging conditions show a similar pattern to that seen for the Jump and Abridging conditions in the main experiment (compare Fig. 5 to Fig. 4). The Abridging condition results in much shorter average gap estimates relative to both the Jump and Occlusion controls.

Discussion

The results confirm our prediction that when a gap in the motion trajectory is traversed in an instant, the gap would appear shorter, or filled-in. Smaller gap sizes filled-in completely and larger ones were judged as much shorter than the same gaps crossed by two-point apparent motion or by an occlusion-like stimulus. The latter result is a replication of the result obtained in touch (Seizova-Cajic & Taylor, 2014; Nguyen et al, 2016).

Note that in all experimental conditions, our target was visible for the same amount of time on both sides of the gap. Motion outside the gap and time across the gap determined how large the gap appears to be.

The gap in our stimulus is a new version of artificial scotoma. An artificial scotoma is an area of a sensory surface deprived of input while a dynamic pattern is shown in the surround (Kapadia, Gilbert, & Westheimer, 1994). The difference between most previously described scotoma-inducing contexts and ours is that our stimulation is *successive* – the stimulus is never present simultaneously on both sides of the gap.

Previous research shows that the filling-in of scotoma occurs gradually during exposure to the surround stimulation, and takes longer for larger scotomas (De Weerd, Gattass, Desimone & Ungerleider, 1995). Experiment 1 results seem consistent with this, judging by the contour plots for Abridging condition in Fig. 3, and the significant effect of Repeats in the LMM analysis, where the average decease in reported gap size over ten repeats was 0.28 dva. This average decrease in the Abridging condition is almost identical to the average decrease for the Jump condition of 0.27 dva, but the ranges across gap sizes are very different: 0.55 for the Abridging vs 0.06 in the Jump condition (compare grey and black bars in Fig 4, right). In the Abridging condition, there is a floor effect: the five smallest gap sizes usually filled-in (see Fig. 3, bottom panels) so they could decrease no further. Larger gaps decreased more than in the Jump condition.

It is not clear why reported gap size decreases in the Jump condition. As suggested by a reviewer, some of the response change may be due to shifts in responses rather than in perception. However, response shift cannot explain the difference between

Abridging and Jump conditions, supporting the presence of a perceptual component in the repetition effect of filling-in.

In Experiment 2 we investigate the effect of exposure on filling-in more closely, by manipulating the exposure within each trial.

Experiment 2. Does filling-in increase with within-trial exposure?

We systematically varied the exposure to our artificial scotomas *within individual trials*: observers saw 1, 3 or 5 up-and-down sweeps of the target across the gap before judging gap size. We also analysed how responses changed as a function of exposure throughout the experimental session as with the factor Repeats in Experiment 1.

Method

Ten participants (4 males, age 20-32, M=23.4) fixated while attending to the peripheral stimulus. After 1, 3 or 5 sweeps, the fixation point disappeared and they adjusted the gap in the probe to match the perceived length of a gap in the motion trajectory observed during the last sweep. With 11 gap sizes, 3 Abridging conditions and 10 repeats, the total number of trials per participant was 330. Trial order was randomised.

Each trial started with a fixation point presented on the left side of the projector screen. Depending on the condition, the stimulus moved along the trajectory only once, or continued its up-and-down motion, crossing the gap three or five times. Gap size was constant within a trial. The subjects were instructed to pay attention to it throughout the trial but to only report the size perceived during the last sweep, before the stimulus disappeared. This was to minimize the chance that reported gap size was that observed at the beginning of the trial.

Temporal characteristics of the stimuli and viewing conditions were the same as in Abridging condition of Experiment 1, except that the moving stimulus was always presented on the right side of the screen. The moving stimulus was shown at 18 dva eccentricity, and the target skipped the gap almost instantaneously, i.e., in 8.3 ms (duration of one frame). A rectangular probe with a gap in the middle, centred at the fixation point, appeared at the start of the trial together with the moving stimulus but became adjustable only after motion sweeps were completed. Response time was not limited.

Data analysis

We again conducted two separate analyses, treating the data as binary and as continuous. Binary data were used to compute the probability of filling-in in different conditions using logistic regression. Only gap sizes smaller than 3 dva were used because five largest gaps were almost never filled-in (see Fig. 6, top).

The second analysis, linear mixed method modelling, was conducted on all gap sizes; raw data were gap size estimates, expressed in degrees of visual angle. We analyzed 33 conditions (3 Number of sweeps x 11 Gap sizes), with participants as a random factor, and 10 trials per participant per condition, for a total of 330 trials per participant. We also tested for cumulative effect across repeated presentation of the same gap size (Repeats), quadratic trends, and interactions. The final model in LMM analysis included three independent fixed factors: Gap size (11 values), Sweeps (1, 3, 5), and Repeats (10 values). The additional fixed factors were Gap size^2, Repeats^2 and four interactions involving Gap size and Repeats (Gap size x Repeats, Gap size^2 x Repeats, Gap size x Repeats^2 and Gap size^2 x Repeats^2). Random factors were inter-participant variations in intercept, slope and curvature of functions relating Gap size to Perceived gap size. Heterogeneous compound symmetry (CSH) variance-covariance matrix structure was used for random effects and for variance of the residuals (G matrix and R matrix, respectively).

Results

Binary data

The probability of filling-in across participants decreased with gap size and increased with the number of sweeps (see contour plots in Fig 6, top). There is no clear increase in filling-in with repetitions. There even seems to be less filling-in for small gap sizes towards the end of the session (repeats 7-10) than at its beginning (for 1 sweep) or middle (3 and 5 sweeps).

Equal-probability thresholds for gap detection were computed for the individual data as a function of number of sweeps in the trial in which the response was made (Fig. 6, bottom). Gaps with 50% chance to be seen (and their SDs) were on average 1.4 (±1.26), 2.2 (±2.1) and 2.0 (±1.0) dva for one, three and five sweeps, respectively. A repeated measures one-way ANOVA showed they were not significantly different from one another (F(2, 18) = 1.51; p = .248). The overall average gap-detection threshold was 1.9 (±1.3) dva.

Gap size estimates

Gap size estimates are shown in Fig. 7. They increase with physical gap size (F(1, 11.0) = 143.0, p < .001), as could be expected. They were also larger for one sweep-stimuli than for three or five sweeps, between which there was little difference

Our main interest was in Sweeps and Repeats, our two ways to operationalize exposure. Factor Sweeps was highly significant (F(2, 438.6) = 17.4, p < .001), carried mainly by the larger gap estimates in the one-sweep condition compared to 3 and 5 sweeps (see top panels of Fig. 7). The mean reported gap sizes following 1, 3 and 5 sweeps were 1.50 (1.23 – 1.76), 1.27 (1.00 – 1.53) and 1.20 (.94 – 1.47) dva, respectively (estimated marginal means and 95% CIs). Results of pairwise comparisons with

Bonferroni correction showed that 1 sweep differed significantly from 3 and 5 sweeps (p < .001), while 3 and 5 sweeps did not significantly differ from one another (p = .547)..
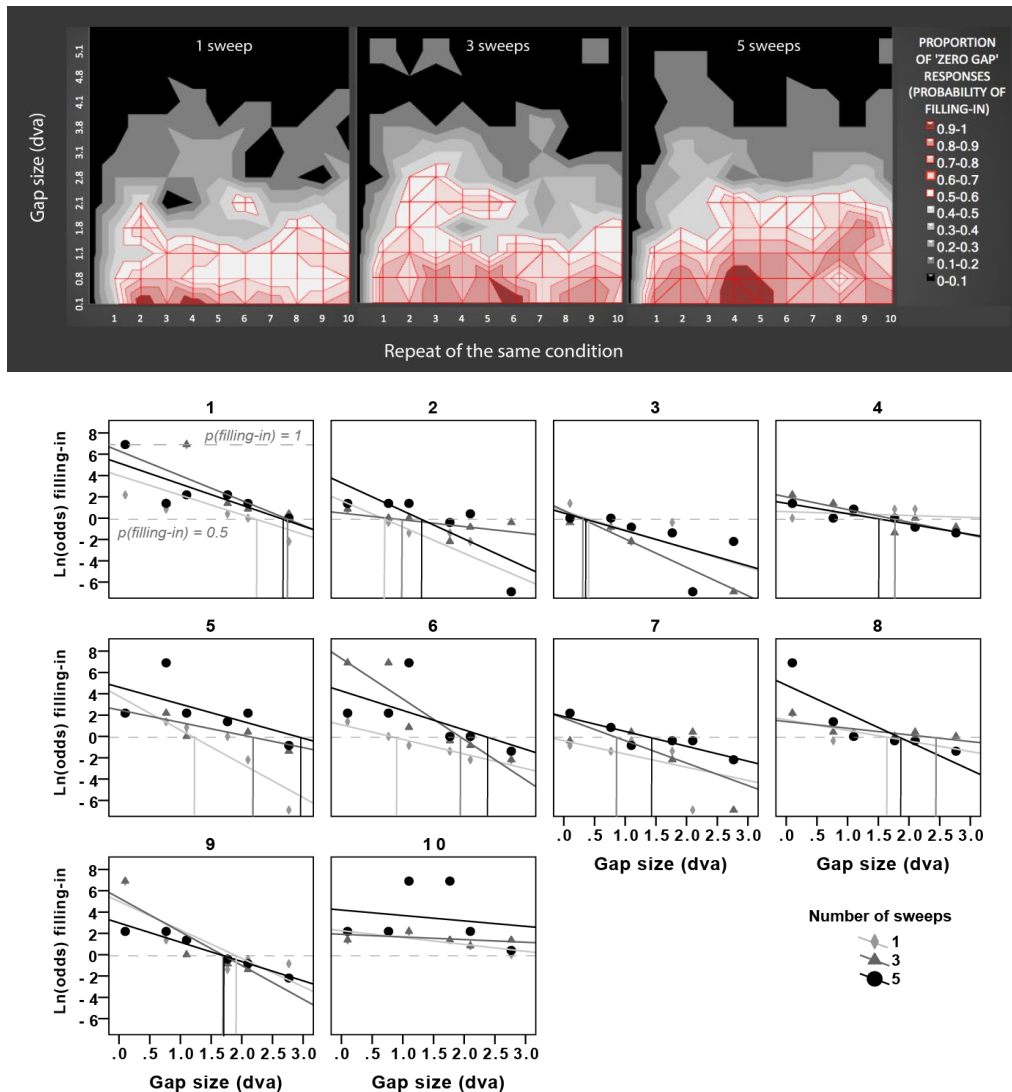

Figure 6. *Top panel*: Probability of filling-in across participants in Experiment 2 (n=10) as a function of exposure, gap size and number of sweeps (1, 3 and 5). Exposure is represented as the number of repeats of the same condition (there were 10 repeats per participant), shown on the x axis. Black fields represent an absence of filling-in, and dark red fields indicate conditions where it occurred at the rate of 0.9 or 1. Outlined areas indicate proportions of 0.5 or higher. *Bottom panel*: Individual psychometric functions showing probability of filling-in (in log odds) as a function of gap size and number of sweeps. The broken horizontal line (ln odds = 0) represents 50% chance of filling-in, and intersecting vertical lines point to the gap sizes with 50% chance of being filled-in (participant 10 filled-in most gaps in the range chosen for this analysis; his/her estimated thresholds are greater than 3 dva). Increasingly darker lines indicate increasing number of sweeps (from 1 to 3 to 5). The trend visible in some plots, where more sweeps fill-in larger gaps (darker lines to the right of lighter lines – participants 1, 2, 5, 6, 7, 8), is not statistically significant at a group level.

14

Factor Repeats was also significant: gap size estimates changed over the course of the experiment, i.e., across repeated presentations of the same stimuli. However, they changed in different ways depending on the physical gap size. For example, responses to 2.1 dva gap decreased throughout the experiment, while response to 5.1 dva increased and then mildly decreased (see bottom left panel of Fig. 7). This is reflected in a significant interaction between quadratic components for Gap size and Repeats ($F(1, 1895.4) = 6.9$, $p = .009$).
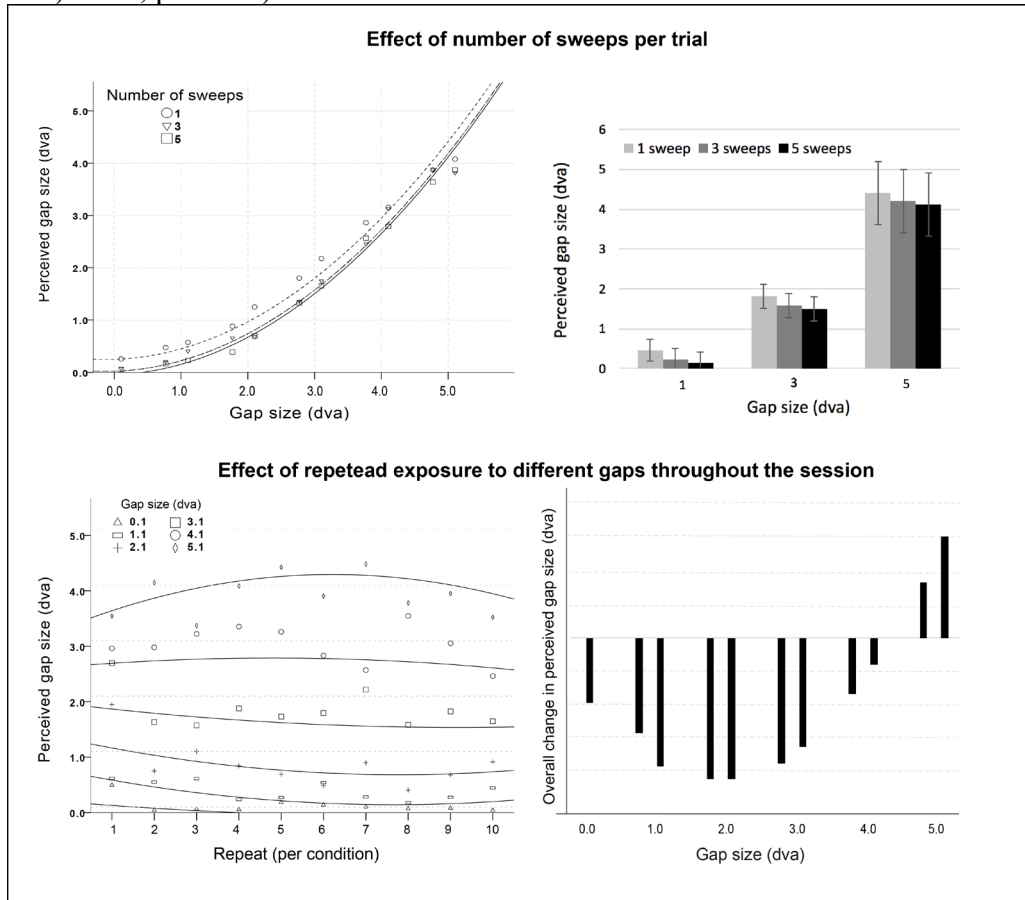
Figure 7. Perceived gap size, Experiment 2 (n=10). *Top*: Perceived gap size as a function of number of sweeps and real gap size. Values shown are estimated marginal means based on the linear mixed model, for all gap sizes (*on the left*) and for three representative gap sizes with 95% CIs for the mean (*on the right*). Note that with increasing number of sweeps, perceived gap size decreases. The difference is statistically significant for 1 sweep vs 3 or 5 sweeps, but not between 3 and 5 sweeps. *Bottom left*: Perceived gap size as a function of gap size and Repeats, estimated marginal means. The x-axis shows only ten repeats although there were 30 repeats per gap (10 each for 1, 3 and 5 sweeps), because we averaged across sweeps; thus, each data point in the plot represents the estimated marginal mean for 10 participants who contributed three data points each. Only six of eleven gap sizes are shown for clarity (0.8, 1.8, 2.8, 3.8 and 4.8 dva gaps are not shown). Note that changes in perceived gap size with Repeats depend on the Gap size. *Bottom right:* An overall change in perceived gap size from the 1st to 10th Repeat, as a function of Gap size (all eleven sizes now shown; the values are based on estimated marginal means). All except the largest two gaps are perceived as smaller at 10th Repeat, with the greatest decrease for 1.8 – 2.1 dva gaps. See text for statistical analysis.

The greatest overall *decrease* in perceived gap size from the 1st to 10th repeat occurred for gaps of approximately 2 dva. Two largest gaps reverse the trend and are seen as a little larger at the end of experimental session than at its beginning.

Discussion

Our results show a small but significant effect of increased exposure on the artificial, motion-defined scotoma: the rate of filling-in increases (see contour plots in Fig 6), and gap size estimates get smaller (Fig. 7, top) with increasing number of sweeps. We only found a significant difference between one sweep and three or five sweeps, but not between the latter two. We only tested the Abridging condition here and cannot claim the effect is specific to the motion context it creates, but different responses to repeats in different motion contexts seen in Experiment 1 suggest it could be.

The effect of exposure *within* each trial (Sweeps) might have been underestimated because there is also cumulative effect *across* trials (Repeats). The latter also results in a decrease in perceived gap size, except for the two largest gaps.

Interestingly, the effect of exposure is greatest for a gap of about 2 dva (Fig. 7, bottom right). It is not surprising that shrinking in absolute terms increases with gap size - smaller gaps have less scope to shrink. Furthermore, small gaps fill-in more easily, even during the first presentation (see contour plots in Fig. 6), leaving less room for further decrease in *average* size (a floor effect). However, gaps beyond 2 dva shrink increasingly less in absolute terms. Why would this be? It may be due to mixing the different gap sizes in the same sessions, affecting how any long term artificial scotoma is built up: the large gaps have significant parts of their "absent" trajectory over locations where the motion is present for shorter gaps. This could explain why large gaps accumulate less change in size, but does not explain why the two largest gaps seem to *expand* in this experiment (not so in Experiment 1). Presenting each gap separately would tease apart changes due to the (repeated) interaction with other gap sizes from those due to the repetition itself.

A reviewer suggested the possibility that could potentially explain both the apparent decrease of small gap sizes and increase of large ones in the present experiment: a general tendency to report more extreme values over the course of the experiment. This cannot be ruled out although the response increase was not observed in Experiment 1 (in that experiment, the upper limit of the range was populated by the responses to the Jump condition, and one would thus expect them to increase for larger gap sizes, which did not happen). Importantly, though, the Abridging and Jump conditions in Experiment 1 behaved differently over the course of each session, with greater response decrease in the Abridging condition for the gap sizes that escaped the floor effect. This suggest a cumulative filling-in effect of the Abridging type of motion.

General discussion

Our Abridging motion stimulus skipped over an area in the middle of the motion path. The result was disappearance or shrinking of the gap compared to gaps defined by

two-point apparent motion or occlusion. This visual effect reproduces the effect of the Abridging stimulus in touch, demonstrated using continuous brush motion on the forearm (Seizova-Cajic & Taylor, 2014; Nguyen et al, 2016), and apparent motion using a pin array on the fingertip (Kaneko et al, 2018). In the visual case, the effect increased with repetition, for most gap sizes.

The Abridging stimulus violates the expectation about target reappearance from behind an occluder. The visual system creates this expectation, an estimate of invisible motion, if the velocity is constant or uniformly changing, and the target is visible for a few hundred milliseconds prior to occlusion (as established using gaze behavior, motion prediction and other measures; see Battaglini, Campana & Casco, 2013, Bosco et al, 2015, and Makin, 2017, for reviews). Both conditions were fulfilled in our experiments, with constant-velocity targets visible for no less than 200 ms before disappearing. Combined with near-zero time to target reappearance from behind an occluder, there is no doubt that the extreme violation created by the Abridging stimulus is easily detected by the visual system. The same is most likely true of the far less studied tactile system.

We used fixation and peripheral presentation in the present study, and 'fixation' with peripheral presentation was also used in the studies in touch (Seizova-Cajic & Taylor, 2014; Nguyen et al, 2016). However, neither seems necessary: gap underestimation and filling-in appear to also occur with smooth pursuit in vision (see Animations 1-3, this time pursuing the moving target), and on a densely innervated fingertip, a tactile equivalent of the fovea (Kaneko et al, 2018).

Perceptual effects of the Abridging pattern described here and in earlier tactile studies resemble those induced by other stimuli. Natural and artificial blind spots are perceptually filled with the dynamic surround (Ramachandran & Gregory, 1991), and motion shifts apparent position of nearby objects (Cavanagh & Anstis, 2013; Eagleman & Sejnowski, 2007; Kohler, Cavanagh & Tse, 2015; Whitney, 2002). We also know that high speed makes the motion path look shorter both in apparent (Geldard, 1976; Kilgard & Merzenich, 1995) and continuous visual motion (Nakajima et al., 2016), as it does in tactile continuous (Whitsel et al, 1986) and apparent motion (Geldard & Sherrick, 1972; Trojan et al, 2010). It is likely that mechanisms responsible for all these effects are also engaged in the present case, but possibly not in the same way, because our stimulus is the first to simulate a rearrangement of the sensory surface and represents a potential trigger for a long-term change. Our first aim is to understand the immediate perceptual effect – gap shrinking and disappearance.

## Why does the gap shrink and disappear?

Decorrelation.
In the case of classical artificial scotoma (Ramachandran & Gregory, 1991; Pessoa & De Weerd, 2003), the gap is filled-in with surrounding stimulation. The term 'filling-in' has a perceptual and neural connotation. Perceptual filling-in, or completion, refers to the observer's "report that something is present in a particular region of visual space when it

is actually absent from that region, but present in the surrounding area" (Pessoa, Thomson & Noe, 1998, p. 723). Neural filling-in refers to the processes of neural interpolation and any other neural process thought to underlie the perceptual filling-in.

Our results satisfy the above definition of perceptual filling-in: rather than correctly perceiving motion trajectory containing a gap (Fig. 8A), our participants often see it as continuous. Our finding that gap shrinking increases with repetition is consistent with the known properties of perceptual filling-in: in natural blind spots, it starts from the edges of a scotoma and may take many seconds to complete (Spillmann, Otte, Hamburger & Magnussen, 2006), and in the artificial scotoma, it takes longer for larger gaps (De Weerd, Gatass, Desimone & Ungerleider, 1995). However, different neural processes may be responsible for different kinds of perceptual filling-in (Pessoa, Thomson & Noe, 1998, p. 723). To distinguish between those, it is instructive to consider the function it fulfils.

The term 'filling-in' implies *there is space to be filled*. Likewise, 'completion', often used interchangeably with filling-in, implies that *input is incomplete*. Neither of the two completely describes our case. In the Introduction we proposed a functional reason for shrinking and eventually removing the gaps that correlate with sudden acceleration: they signal that something is wrong with the sensory system, and in particular, that it has a surplus receptor area that has no corresponding area in the input space. A similar
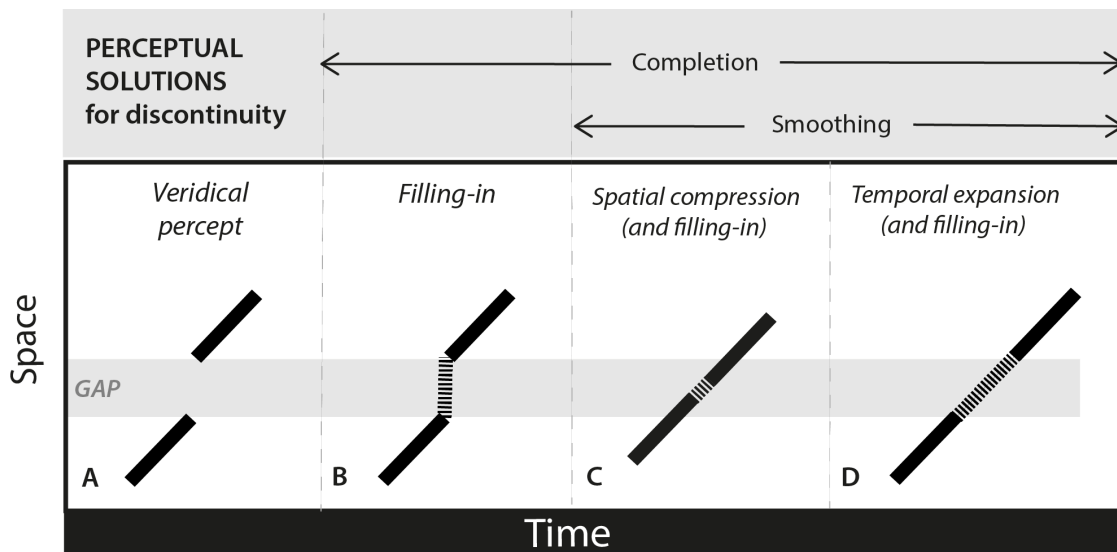
Figure 8. Space-time diagrams of in-principle perceptual solutions of the Abridging stimulus. The GAP represents receptor area deprived of input; broken line represents filling-in i.e., interpolation of motion across the gap between two co-directional sweeps. **A**. Veridically perceived Abridging stimulus would appear as constant-velocity target that jumps a spatial gap instantaneously, or disappears at the gap, with a different target appearing on the other side. **B**. Filling-in: the motion trajectory is complete but contains sudden acceleration. **C**. Spatial compression and filling-in: positions on the two sides of the Gap appear closer together, and the *remaining* gap area is filled-in; the motion trajectory is complete and velocity is constant i.e., spatiotemporal trajectory is smooth. **D**. Temporal expansion and filling-in: the time interval during which the target is not visible is perceptually expanded, and space is filled-in; the motion trajectory is again complete and velocity constant.

functional explanation was put forward regarding the fading effect that involves motion (Motion-Induced-Blindness, MIB). New and Scholl (2008) proposed that a lack of change in a small area in the visual field during surround motion is treated by the visual system as an artifact of damage, a scotoma, and thus discounted. However, while in the case of MIB or classical scotoma, the stimulus is discounted and space preserved and filled-in, we propose here that *space itself has to go.*

If this is the task of the perceptual system when presented with the Abridging stimulus, the criterion for its completion is the decorrelation (Barlow & Foldiak, 1989) between acceleration and gaps in stimulation, resulting in a smooth average motion trajectory. This would not be achieved instantaneously but only after prolonged exposure to the Abridging stimulus of the same receptor area. If our hypothesis is correct, filling-in of the existing sensory space (illustrated in Fig. 8B) cannot be the only process involved because it does not smooth the trajectory.

The smoothing would occur if *the representation of the spatial extent containing the gap shrank* (Fig. 8C). We included in this solution an arbitrary amount of filling-in (broken line in Fig. 8C) to illustrate that any combination of spatial compression and filling-in is possible, and we expect their ratio to change in favour of compression with exposure. Note that the perceived positions of locations surrounding the gap should change with compression. Tactile studies on the forearm found localization errors consistent with this prediction (Seizova-Cajic & Taylor, 2014; Nguyen et al, 2016).

A smooth trajectory can also ensue if *the representation of duration of the target's disappearance expanded* (Fig. 8D). In this case, the spatial gap would not shrink and would need to be filled-in (broken line in Fig. 8D). Our illustrations are simplistic; we do not suggest that space compression and time expansion are mutually exclusive or even distinct options. As Burr & Thompson (2011) noted regarding the influence of motion on position, "the debate often stagnates on issues like whether the effects result from distortions to space or to time, [yet] it should be now clear that space and time are not neatly separable for motion, so the distinction is moot." (p. 1442).

In summary, filling-in is not enough. Other changes need to occur to smooth out the motion trajectory and separate (de-correlate) the gap in stimulation from sudden accelerations. What changes at the neural level would support this decorrelation is not yet clear.

Decorrelation, or just spatial compression?

The Abridging stimulus contains within it a sub-pattern that causes a significant spatial compression, the two-point version of sensory saltation, known as the 'utterly reduced rabbit' (Geldard, 1975, 1976). It consists of two points (in vision) or taps (in touch) presented for a short time only and in quick succession (Fig. 9). The perceptual effect is spatial compression of inter-stimulus distance, which increases with shortening of the inter-stimulus interval. Example tactile patterns that result in large spatial compression are 5 to 100-ms taps presented with 100-ms stimulus onset asynchrony (Geldard, 1975; Geldard & Sherrick, 1972; Kilgard & Merzenich, 1995; Trojan et al, 2010). In vision, Geldard obtained the rabbit illusion with flashes lasting from 2-5 ms to 100 ms (Geldard,

1975). Spatial compression observed in this type of stimuli has been linked to similar effects in other high-velocity stimulus configurations, and attributed to a low-velocity prior (Goldreich & Tong, 2013).

This impoverished stimulus is contained within the Abridging pattern, where it marks the endpoints of motion sweeps adjacent to the gap and connected by a sudden acceleration (Fig. 9B). Can it explain the gap-shrinking effects induced by the Abridging stimulus?

We think not. Local features of any rich stimulus interact with the context, and how they are perceived depends on the context (Wertheimer, 1923/1964; Todorovic, 2011). As Fig 9A shows, sensory saltation is also contained within our Jump control condition, which resulted in far less spatial compression than the Abridging stimulus. We also informally explored the effect of context by using different motion patterns. Animation 4 (also see Fig. 9C) demonstrates that the context dramatically affects perceived gap size in a manner consistent with our explanation. In Animation 4, rather than a single moving object, *two* objects are presented on opposite sides of the gap and the gap no longer seems compressed, although the saltation stimulus is still locally present.
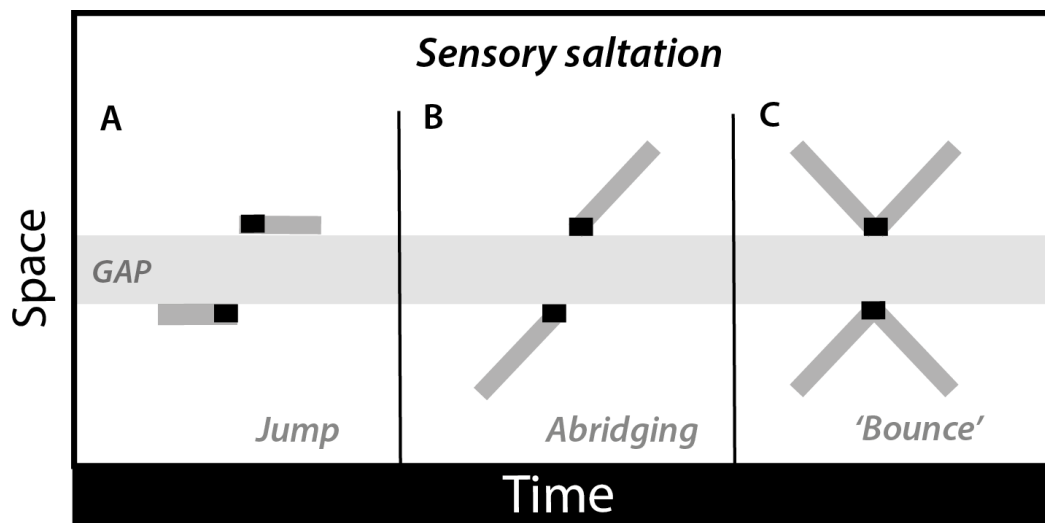
Figure 9. A two-point version of sensory saltation stimulus (black squares) superimposed on (A) our Jump stimulus, (B) the Abridging stimulus and (C) a new, 'Bounce' stimulus (thick grey lines). Our Jump stimulus was presented for approximately 230 ms on each side of the gap and resulted in approximately 10% compression for 5.1 dva gap size (see Fig. 4). With shorter presentation time, it would become a saltation stimulus itself. A roughly comparable stimulus lasting only 2-5 ms resulted in 50% spatial compression (estimated from Fig. 19 in Geldard, 1975, for the stimulus at 20 dva eccentricity, 5 dva gap size, with 50 ms inter-stimulus interval). The 50% compression is similar to that obtained in our Abridging condition (5.1 dva gap size, Fig. 4). See text and Animation 4 for more details regarding the Bounce stimulus.

Why is this consistent with our decorrelation explanation? By adding another moving object, we eliminated the need to bind motions on two opposite sides of the gap. Each object appears to bounce off an invisible boundary and continues moving on its own side. Since no object crosses the gap, there is no sudden acceleration, and no need for decorrelation between gap location and acceleration. Thus, the gap can be seen in its full size. Some observers also report an alternative perceptual solution (for Animation 4), making this a bistable stimulus: each of the two objects continues along its trajectory, crossing to the opposite side. In that case, the usual compression of the perceptual gap occurs. In Animations 5 and 6 we used colour to influence perceived target trajectories, which should result in 'bouncing' and 'streaming' (cross-over) motions, respectively (Kawachi, Kawabe & Gyoba, 2006). These observations, yet to be tested in formal experiments, suggest that the broader motion context and perceptual organization strongly modulate gap shrinking and filling-in.

Both our decorrelation explanation and the proposal of a low-velocity constraint (Goldreich & Tong, 2013) offer reasons why sudden accelerations are 'removed' from the percept. However, the decorrelation account has two advantages: it does not require priors, and it relies on known principles of perceptual organization.

The Abridging paradigm as a tool for study of motion-driven plasticity

The Abridging paradigm provides a simple experimental tool to explore the possible role of motion in plasticity of sensory maps in conscious humans. Psychophysical findings support the idea that local motion detectors facilitate their neighbours in a predictive fashion, in the direction of motion; this seems to be true for straight motion trajectories, or trajectories with small curvature (Watamaniuk, McKee & Grzywacz, 1995). If the Abridging paradigm has such an effect on spatially remote retinal points, then prolonged exposure to it may shift the position signals for neurons whose receptive fields are located there.

More precisely, we hypothesize that repetitive leaps across the gap gradually create predictive facilitation of the receiving, remote local motion detector on the other side of the gap. At the same time, they trigger filling-in of the deprived area. The two processes are in *competition*, given that filling-in reaffirms there is an area to be filled, while remote connecting requires the area in-between to disappear from the map. Over time, their balance shifts in favour of the latter process, until eventually neurons on the two sides of the gap become functional neighbours with an altered position signal each.

Neural mechanisms that might support these processes include strengthening of synapses between sequentially stimulated neurons, weakening of synapses among neurons no longer connected by motion, disinhibition of long-range lateral connections between cortical neurons with similar response properties, recurrent feedforward and feedback connections between local motion detectors and higher-order neurons with larger receptive fields, and restructuring of input to the cortex (these mechanisms were discussed in different contexts by the following authors: Buonomano & Merzenich, 1998;

De Weerd, 2006; Detorakis & Rougier, 2012; Gilbert & Li, 2012; Sheridan, 2015; Spillmann, Dresp-Langley & Tseng, 2015; Yantis & Nakama, 1998).

The evidence gathered in animal research also points to a significant role of motion in establishment of sensory maps. Before the eyes are even exposed to light, waves of spontaneous neural activity sweep across the retina refining visual circuits set in place by other processes; if this process is disturbed, so are the retinal maps (see Kirkby et al., 2013 for review). Disturbance of the orderly optic flow stimulation during early development has a similar effect in tadpoles (Hiramoto & Kline, 2014).

Conclusion

Unlike artificial scotomas that make visual or tactile receptor surface *insentient*, our motion-gap (Abridging) pattern suggests that a portion of the receptor surface has been excised and the edges left behind stitched together*,* making it a potentially useful tool in the experimental study of plasticity in sensory maps. It has similar effects in vision and touch, but the two sensory modalities offer distinct advantages for further study. Control over stimulus placement is much easier in touch than vision, where eye movements need to be monitored, and allows use of longer-lasting stimuli. Visual displays, on the other hand, make it easy to vary stimulus features and other presentation parameters. We expect insights from the two lines of research to complement each other in the exploration of motion-induced plasticity in spatial maps.

Acknowledgments:

References

Awater, H., Kerlin, J.R., Evans, L.K., & Tong, F. (2005). Cortical Representation of Space Around the Blind Spot. *Journal of Neurophysiology*, 94(5), pp.3314–3324. http://www.physiology.org/doi/10.1152/jn.01330.2004.

Barlow, H.B. & Földiák, P. (1989). Adaptation and decorrelation in the cortex. *The Computing Neuron*, (1988), pp.54–72.

Battaglini, L., Campana, G., & Casco, C. (2013). Illusory speed is retained in memory during invisible motion. *i-Perception*, *4*(3), 180-191. https://doi.org/10.1068/i0562

Boring, E.G. (1950). *A history of experimental psychology*. Appleton-Century-Crofts, New York.

Brooks, J., Seizova-Cajic T., Taylor J. L. (2015). Motion across a tactile scotoma shifts perceived position. *Presentation at the Conference of the Australasian Society for Experimental Psychology* (Sydney, NSW).

Buonomano, D. V, & Merzenich, M. M. (1998). Cortical Plasticity: From Synapses to Maps. *Annual Review of Neuroscience*, *21*, 149–86. doi: 10.1146/annurev.neuro.21.1.149

Burr, D. & Thompson, P. (2011). Motion psychophysics: 1985-2010. *Vision Research*, 51, pp.1431–1456. http://www.ncbi.nlm.nih.gov/pubmed/21324335.

Calford, M.B., Clarey J.C. & Tweedale, R. (1998) Short-term plasticity in Adult Somatosensory Cortex. Morley, J. (Ed) *Neural Aspects of Tactile Sensation*. North-Holland.

Cavanagh, P., & Anstis, S. (2013). The flash grab effect. *Vision Research*, *91*, 8–20. http://doi.org/10.1016/j.visres.2013.07.007

Chun, M. M., & Cavanagh, P. (1997). Seeing two as one : Linking apparent motion and repetition blindness. *Psychological Science*, *8*(2), 74–79. http://dx.doi.org/10.1111/j.1467-9280.1997.tb00686.x

Clark, S., Allard, T., Jenkins, W., & Merzenich, M. (1988). Receptive fields in the body-surface map in adult cortex defined by temporally correlated inputs. *Nature*, *332*(31), 444–5. doi:10.1038/332444a0

del Rio, T. & Feller, M.B. (2006). Early Retinal Activity and Visual Circuit Development. *Neuron*, 52(2), pp.221–222. https://doi.org/10.1016/j.neuron.2006.10.001

Detorakis, G.I. & Rougier, N.P. (2012). A neural field model of the somatosensory cortex: Formation, maintenance and reorganization of ordered topographic maps. *PLoS ONE*, 7(7). https://doi.org/10.1371/journal.pone.0040257

De Weerd, P. (2006). Perceptual filling-in: More than the eye can see. *Progress in Brain Research*, 154, pp.227–45. http://www.ncbi.nlm.nih.gov/pubmed/17010714

De Weerd, P., Gatass, R., Desimone, R. & Ungerleider, L. (1995). Responses of cells in monkey visual cortex during perceptual filling-in of an artificial scotoma. *Nature*, 377, pp.731–734. doi: 10.1038/377731a0

Feldman, J. & Tremoulet, P.D., (2006). Individuation of visual objects over time. *Cognition*, 99(2), pp.131–165. doi:10.1016/j.cognition.2004.12.008

Eagleman, D. M., & Sejnowski, T. J. (2007). Motion signals bias localization judgments: A unified explanation for the flash-lag, flash-drag, flash-jump and Frohlich illusions. *Neurobiology*, *7*, 1–12. http://doi.org/10.1167/7.4.3.

Geldard, F. A. (1975) *Sensory Saltation: Metastability in the Perceptual World*. Lawrence Erlbaum Associates, Hillsdale, NJ.

Geldard, F. A. (1976). The saltatory effect in vision. *Sensory Processes*, *1*, 77–86.

Geldard, F. & Sherrick, C.E. (1972). The cutaneous "rabbit": a perceptual illusion. *Science (New York, N.Y.)*, 178(4057), pp.178–9. http://www.ncbi.nlm.nih.gov/pubmed/5076909.

Goldreich D, Tong J (2013) Prediction, postdiction, and perceptual length contraction: a Bayesian low-speed prior captures the cutaneous rabbit and related illusions. *Frontieres in Psychology* 4: 221. doi: 10.3389/fpsyg.2013.00221

Hiramoto, M. & Cline, H.T. (2014). Optic flow instructs retinotopic map formation through a spatial to temporal to spatial transformation of visual information. *Proceedings of the National Academy of Sciences of the United States of America*, 111(47), pp.E5105–E5113. http://www.ncbi.nlm.nih.gov/pubmed/25385606

Kanai, R., Sheth, B. R., & Shimojo, S. (2007). Dynamical evolution of motion perception. *Vision Research 47* (7), 937–945. http://doi.org/10.1016/j.visres.2006.12.009

Kaneko S., Kajimoto H., Hayward V. (2018) A Case of Perceptual Completion in Spatio-Temporal Tactile Space. In: Prattichizzo D., Shinoda H., Tan H., Ruffaldi E., Frisoli A. (eds) *Haptics: Science, Technology, and Applications. EuroHaptics 2018. Lecture Notes in Computer Science,* vol 10893. Springer, Cham.

Kapadia, M., Gilbert, D. & Westheimer, G. (1994). Measure for Short-term Cortical Plasticity in Human Vision. *The Journal of Neuroscience*, 14, pp.451–457. https://www.ncbi.nlm.nih.gov/pubmed/8283250

Kawachi, Y., Kawabe, T. & Gyoba, J., (2011). Stream/bounce event perception reveals a temporal limit of motion correspondence based on surface feature over space and time. *i-Perception*, 2(5), pp.428–439. doi: 10.1068/i0399

Kilgard, M. P., & Merzenich, M. (1995). Anticipated stimuli across skin. *Nature*, *373*(6516), 663. http://doi.org/10.1038/373663a0

Koenderink, J.J., (1990). The brain a geometry engine. *Psychological Research*, 52, pp.122–127. https://doi.org/10.1007/BF00877519

Kohler, P. J., Cavanagh, P., & Tse, P. U. (2015). Motion-induced position shifts are influenced by global motion, but dominated by component motion. *Vision Research*, *110*, 93–99. http://doi.org/10.1016/j.visres.2015.03.003

Makin, A.D.J. (2017). The common rate control account of prediction motion. *Psychonomic Bulletin & Review*. https://doi.org/10.3758/s13423-017-1403-8

Maloney, L.T. & Ahumada, A.J. (1989). Learning by Assertion: Two Methods for Calibrating a Linear Visual System. *Neural Computation*, 1(3), pp.392–401. http://www.mitpressjournals.org/doi/10.1162/neco.1989.1.3.392.

Maus, G. W., & Whitney, D. (2016). Motion-dependent filling-in of spatiotemporal information at the blind spot. *PLoS ONE*, *11*(4), 1–14. http://doi.org/10.1371/journal.pone.0153896

McGraw, P. V, Walsh, V., & Barrett, B. T. (2004). Motion-Sensitive Neurones in V5/MT Modulate Perceived Spatial Position. *Current Biology*, *14*, 1090–1093. http://doi.org/10.1016/j

Merzenich, M. M., & Jenkins, W. M. (1993). Reorganization of Cortical Representations of the Hand Following Alterations of Skin Inputs Induced by Nerve Injury , Skin Island Transfers , and Experience. *Journal of Hand Therapy*, *6*(2), 89–104. http://doi.org/10.1016/S0894-1130(12)80290-0

Nakajima, Y., Sakaguchi, Y., Livingstone, M. S., Hubel, D. H., Livingstone, M. S., Hubel, D. H., … Sakaguchi, Y. (2016). Perceptual shrinkage of a one-way motion path with high-speed motion. *Scientific Reports*, *6*(July), 30592. http://doi.org/10.1038/srep30592

New, J.J. & Scholl, B.J. (2008). "Perceptual scotomas": A functional account of motion-induced blindness: Research article. *Psychological Science*, 19(7), pp.653–659. https://doi.org/10.1111/j.1467-9280.2008.02139.x

Nguyen, E. H. L., Taylor, J. L., Brooks, J., & Seizova-Cajic, T. (2016). Velocity of motion across the skin influences perception of tactile location. *Journal of Neurophysiology*, *115*, 674–684. http://doi.org/10.1152/jn.00707.2015

Pessoa, L., & De Weerd, P. (2003). *Filling In: From Perceptual Completion to Cortical Reorganization.* Oxford: Oxford University Press.

Pessoa, L., Thompson, E., & Noë, A. (1998). Finding out about filling-in : A guide to perceptual completion for visual science and the philosophy of perception. *Behavioral and Brain Sciences*, *21*, 723–802. Retrieved from: https://www.ncbi.nlm.nih.gov/pubmed/10191878

Ramachandran, V. S., & Gregory, R. L. (1991). Perceptual filling in of artificially induced scotomas in human vision. *Nature*, *350*(6320), 699–702. http://doi.org/10.1038/350699a0

Seizova-Cajic, T., & Taylor, J. L. (2014). Somatosensory space abridged: Rapid change in tactile localization using a motion stimulus. *PLoS ONE*, *9*(3). http://doi.org/10.1371/journal.pone.0090892

Sheridan, P. (2015). Long-range cortical connections give rise to a robust velocity map of V1. *Neural Networks*, *71*, 124–141. http://doi.org/10.1016/j.neunet.2015.08.005

Spillmann, L., Dresp-Langley, B., & Tseng, C. (2015). Beyond the classical receptive field : The effect of contextual stimuli. *Journal of Vision*, *15*(9), 1–23. http://doi.org/10.1167/15.9.7.doi

Spillmann, L., Otte, T., Hamburger, K., & Magnussen, S. (2006). Perceptual filling-in from the edge of the blind spot. *Vision Research*, *46*(25), 4252–4257. http://doi.org/10.1016/j.visres.2006.08.033

Todorović, D. (2011). What is the Origin of the Gestalt Principles? *Humana Mente Journal of Philosophical Studies*, *17*, 1–20. https://www.scribd.com/document/137324725/Humana-Mente-17-the-Legacy-of-Gestalt-Psychology

Trojan, J., Stolle, A.M., Mrsic Carl, A., Kleinbohl, D., Hong, Z.T., & Holzl, R. (2010). Spatiotemporal integration in somatosensory perception: effects of sensory saltation on pointing at perceived positions on the body surface. *Frontiers in Psychology*, 1(December), p.206. http://www.pubmedcentral.nih.gov/articlerender.fcgi?artid=3153812&tool=pmcentrez&rendertype=abstract

Yantis, S. & Nakama, T., 1998. Visual interactions in the path of apparent motion. *Nature Neuroscience*, 1(6), pp.508–512. doi: 10.1038/2226

West B.T., Welch K.B. & Galecki, A.T. (2015.) *Linear Mixed Models: A Practical Guide Using Statistical Software,* 2nd Edition. CRC Press.

Whitney, D. (2002). The influence of visual motion on perceived position. *Trends in Cognitive Sciences*, *6*(5), 211–216. http://www.sciencedirect.com/science/article/pii/S1364661302018879

Whitsel, B.L., Franzen, O., Dreyer, D., Hollins, M., Young, M., Essick, G.K. & Wong, C. (1986). Dependence of Subjective Traverse Length on Velocity of Moving Tactile Stimuli. *Somatosensory Research*, 3(3), pp.185–196. https://www.ncbi.nlm.nih.gov/pubmed/3749661

Wertheimer M. (1923, 1964) Principles of perceptual organization. In: *Readings in Perception,* edited by Beardslee D, Wertheimer M. New York: van Nostrand.

Animations

Animation 1. 'Abridging' (the critical condition)

The white dot moves back and forth, instantaneously crossing the invisible gap in the middle of its trajectory. Although the spatial gap creates a discontinuity in motion, the trajectory may appear smooth and uninterrupted. The size of the gap is around one sixth of the total length of the trajectory, which is similar to the 2.5 dva gap condition in Experiment 1. Fixate the black dot and watch on repeat (loop) for best effect.

Animation 2. 'Jump' (control condition)

The white dot alternates between the two locations creating an apparent motion effect. The size of the gap as well as the temporal profile of the stimulation is identical to the Animation 1, but the gap between the two locations is clearly visible.

Animation 3. 'Occlusion' (additional control)

The white dot moves back and forth at a constant velocity, disappearing and reappearing from behind an invisible occluder in the middle of its trajectory. The size of the occluder/gap as well as the velocity during the visible motion is identical to the Animation 1, and the only difference is the time it takes for the dot to reappear. Here the gap is clearly visible and the motion always appears interrupted in the middle.

Animation 4. Two-dots stimulus

Two white dots move up and down at a constant velocity, out of phase, each on its own side of an invisible horizontal separator in the middle (a 'wall'). They usually appear to be bouncing off the separator. An alternative percept is that each of the dots disappears behind the separator (an 'occluder') and reappears on the other side. Although physically the same, the wall may appear larger than the occluder, consistent with our interpretation of the Abridging effect: if each dot moves on its own side, and neither crosses the occluder, there is no trigger for spatial compression. See Discussion for more details.

Animation 5. 'Bounce'

Same as Animation 4, except that dots are coloured red and green, with each colour remaining on one side of the gap; this makes the dots look like they bounce off the separator, i.e., increases the chance of the first perceptual solution of Animation 4.

Animation 6. 'Streaming'

Same as Animation 5, except that colours switch sides, making the dots look like they cross the gap (the second perceptual solution of Animation 4).

Tatjana Seizova-Cajic is a Senior Lecturer at the University of Sydney. She completed an undergraduate degree in Psychology and a Masters degree (advisor: Dejan Todorovic) at the University of Belgrade, followed by a PhD in 2003, at the University of New South Wales, Sydney (advisor: Barbara Gillam). Tatjana has held academic positions at her current University since 2002, first at the School of Psychology and then at the Faculty of Health Sciences. Trained in vision, she also investigated touch and proprioception, focusing often on phenomena common to different modalities, such as adaptation and perception of motion. She currently investigates plasticity of visual and somatosensory maps, and perception of self-touch.

Nika Adamian is a Research Fellow at the School of Psychology at the University of Aberdeen. In 2017, she received a PhD in Cognitive Science from Université Paris Descartes, where she studied spatial attention and motion-induced position illusions. Her research interests also include perceptual decision making and temporal dynamics of attention.

Patrick Cavanagh is a Senior Research Fellow at Glendon College and a research professor at Dartmouth College. He received an undergraduate degree in Electrical Engineering from McGill University in 1968 and a PhD in Cognitive Psychology from Carnegie-Mellon University in 1972 and taught at the Université de Montréal from 1972 to 1989, Harvard University from 1989 to 2007, Université Paris Descartes from 2007 to 2017. His current projects study visual attention and the coding of position. He has also explored the contribution of various features such as shadow, color, motion, and texture to representations of visual form and these experiments led to his interest in art as a source of data for neuroscience.