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1 Temporal dynamics of mirror-symmetry perception

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6 Abstract

7 Recent studies have suggested that temporal dynamics rather than symmetrical
8 motion-direction contribute to mirror-symmetry perception. Here we investigate temporal
9 aspects of symmetry perception and implicitly, its temporal flexibility and limitations, by
10 examining how symmetrical pattern elements are combined over time. Stimuli were dynamic
11 dot-patterns consisting of either an on-going alternation of two images (sustained stimulus
12 presentation) or just two images each presented once (transient stimulus presentation)
13 containing different amounts of symmetry about the vertical axis. We varied the duration of
14 the two images under five temporal-arrangement conditions: (1) '*whole patterns*' in which a
15 symmetric pattern alternated with a noise pattern; (2) '*delayed halves*' – the halves of the
16 symmetric and noise patterns were presented with temporal delay; (3) '*matched-pairs*' – two
17 alternating images each containing equal amounts of symmetrical matched-pairs; (4) '*delayed*
18 *matched-pairs*' – the same as arrangement 3, but with matched-pairs presented with delay;
19 (5) '*static*' – both images presented simultaneously as one. We found increased sensitivity in
20 sustained compared to transient stimulus presentations and with synchronous compared to
21 delayed matched-pairs stimuli. For the delayed conditions, sensitivity decreased gradually
22 with longer image durations (>60ms), prominently for the transient stimulus presentations.
23 We conclude that correlations across-the-symmetry-midline can be integrated over time
24 (~120ms) and symmetry mechanisms can tolerate temporal delays between symmetric dot-
25 pairs of up to ~60ms.

26 Keywords

27 Symmetry, temporal delay, temporal integration, psychophysics, perceptual organisation

28 Introduction

29 Mirror symmetry (henceforth ‘symmetry’) is a ubiquitous visual feature in natural
30 images that occurs when one half of an image reflects the other about an axis. Symmetry is a
31 salient visual feature found in both natural and man-made objects, to which the human visual
32 system is highly sensitive. Psychophysical, computational and brain imaging (fMRI) studies
33 have shown that symmetry plays an important role in perceptual organisation (i.e. figure-
34 ground segregation) (Driver, Baylis, & Rafal, 1992; Machilsen, Pauwels, & Wagemans, 2009;
35 Makin, Rampone, Wright, Martinovic, & Bertamini, 2014; Metzger, 2009), object recognition
36 (Pashler, 1990; Vetter & Poggio, 1994; Vetter, Poggio, & Bulthoff, 1994), amodal completion
37 (Saiki, 2000; van Lier, Vanderhelm, & Leeuwenberg, 1995), and visual search (Wolfe &
38 Friedmanhill, 1992) and, involves an extensive network of extra-striate visual areas such as
39 V3a, V4, V7 and LOC (Sasaki, Vanduffel, Knutsen, Tyler, & Tootell, 2005; Tyler et al., 2005).
40 Although several recent studies have examined the contribution of simple visual attributes,
41 such as luminance-polarity and colour (Gheorghiu, Kingdom, Remkes, Li, & Rainville, 2016;
42 Morales & Pashler, 1999; Wu & Chen, 2014), stereoscopic depth (Erkelens & van Ee, 2007;
43 Ishiguchi & Yakushijin, 1999; Treder & van der Helm, 2007), and motion direction (Sharman
44 & Gheorghiu, 2017) to symmetry perception, little or nothing is known about the temporal
45 dynamics of symmetry perception. While recent studies have suggested that temporal
46 dynamics contribute to mirror-symmetry perception (Sharman & Gheorghiu, 2017), none
47 have considered temporal aspects of symmetry perception in *dynamic* stimuli. In this
48 communication, we investigate sustained and transient properties of symmetry perception
49 about vertical axis by examining how symmetrical pattern-elements are combined over time,
50 and whether symmetry mechanisms can tolerate temporal delays between matched
51 elements. By studying both sustained and transient aspects of symmetry perception, one can
52 gain insight into the temporal characteristics of the mechanisms underlying symmetry
53 perception and implicitly, about their temporal flexibility and limitations.

54 Psychophysical and neurophysiological studies indicate that temporal information
55 plays a critical role in many visual processes such as stereoscopic depth (Gheorghiu &
56 Erkelens, 2005a, 2005b), form (Eriksen & Collins, 1967; Niimi, Watanabe, & Yokosawa, 2008;
57 Sharman & Gheorghiu, 2017), and motion (Burr, 1981; Burr & Santoro, 2001) perception.
58 Specifically, it appears that two temporal factors are of major importance for visual

59 perception, namely *duration* and *synchronisation* (i.e. simultaneity of presentation) between
60 corresponding or matched stimulus parts or elements. With regard to duration, many visual
61 features, which require integration across space, can be perceived with only very short
62 stimulus durations. For example, stereopsis (i.e. disparity-defined depth) can be perceived in
63 random-dot stereograms with very brief presentation durations between 1ms (Uttal, Davis,
64 & Welke, 1994) and 60ms (Gheorghiu & Erkelens, 2005a, 2005b; Uttal, Fitzgerald, & Eskin,
65 1975). Similarly, the perception of motion streaks requires stimulus durations of at least 77ms
66 (Alais, Apthorp, Karmann, & Cass, 2011). As for symmetry, this can be reliably detected at the
67 fixation point in static stimuli presented for as short as 30 to 50ms (Julesz, 1971; Tyler,
68 Hardage, & Miller, 1995) although most studies of symmetry perception use stimulus
69 durations of about 400-500ms (Gheorghiu et al., 2016; Sharman & Gheorghiu, 2017; Wu &
70 Chen, 2014, 2017). Using symmetric textures, Cohen and Zaidi (2013) found *temporal*
71 thresholds for identifying the *orientation* of symmetry axis that range between 28 to 568ms.
72 Thus, observers can perceive symmetry even though these stimulus durations do not allow
73 for sequential examination of individual symmetric pairs (Niimi et al., 2008; Tyler et al., 1995;
74 Wagemans, 1995). Furthermore, Treder and van der Helm (2007) examined the interaction
75 between symmetry detection and stereoscopic depth mechanisms by using static stimuli in
76 which symmetrical matched-pairs were distributed either on the same or different depth
77 planes and presented for various durations between 200ms and 1sec. These authors reported
78 that the efficient detection of symmetry in stereoscopic vision depends on structural
79 correspondences within depth planes and requires longer stimulus durations, while
80 symmetry for short presentation durations (200ms) relies on monocular mechanisms.

81 Other studies, however, used unlimited stimulus presentations and measured
82 reaction times for detecting symmetry in non-isoluminant patterns made of two and four
83 colours (Morales & Pashler, 1999). Morales and Pashler (1999) found longer and less accurate
84 responses to the four-colour (2 sec) than two-colour (1.2 sec) patterns, thus arguing that
85 symmetry in multi-colour patterns could only be detected by switching attention from one
86 colour to the next and assessing individually the symmetry for each colour. In sum, the use of
87 either briefly presented static stimuli or an unlimited stimulus presentation time allowing
88 sequential examination of symmetrical pairs does not reflect the time period over which the
89 visual system integrates symmetrical pairs, i.e. computes correlations across the symmetry-

90 midline over time. Instead these durations might reflect the minimum time needed to detect
91 a perceptual change in the stimulus. Recent studies have suggested that symmetry is subject
92 to a cumulative temporal process, where weak symmetry signals are combined together over
93 time to form a relatively stronger response (Niimi et al., 2008; Sharman & Gheorghiu, 2017).
94 There are, however, no studies that have *directly* examined how symmetry mechanisms
95 integrate matched-pairs across the symmetry axis over time in dynamic stimuli.

96 It has been suggested that when studying temporal properties, it is important to
97 distinguish between *transient* (i.e. brief stimulus exposures in which each image is only
98 presented once) and *sustained* (i.e. longer stimulus durations in which the images are
99 continuously alternated) *stimulus presentations* as these two forms of presentation may be
100 mediated by distinct underlying mechanisms (Edwards, Pope, & Schor, 1999; Gheorghiu &
101 Erkelens, 2004; Pope, Edwards, & Schor, 1999; Schor, Edwards, & Pope, 1998). Evidence for
102 separate *sustained and transient mechanisms* comes from stereo-vision domain where it has
103 been suggested that spatially complex stimuli (e.g. dot patterns) can only be processed by the
104 sustained system (Pope et al., 1999). For clarity, the terms *transient* and *sustained* can refer
105 to the type of stimulus presentation, to the underlying mechanism or to the percept. Hence,
106 in this study we will examine symmetry perception in response to both sustained (i.e.
107 prolonged) and transient stimulus presentations. A sustained stimulus presentation allows
108 the visual system to integrate weak symmetry signals over time, within a specific time
109 window, while a transient stimulus presentation allows for a decay in the strength of the
110 symmetry signals over time. This predicts increased sensitivity to symmetry for sustained
111 compared to transient stimulus presentations, and for higher than lower alternation
112 frequencies.

113 By studying sustained and temporal properties of symmetry perception in dynamic
114 stimuli, one can gain insight into how symmetry mechanisms integrate matched-pairs across
115 the symmetry axis and *across time*. Thus, one important temporal factor that can influence
116 how a stimulus is perceived is the synchronisation or simultaneity of presentation of spatially-
117 correlated or matched stimulus elements. For example, it is known that synchronisation of
118 the left and right eyes' images plays an important role in disparity-defined depth perception
119 (Gheorghiu & Erkelens, 2005b). However, disparity-defined depth can also be perceived when
120 one retinal image is somewhat delayed relative to the other, a phenomenon referred to as

121 *tolerance for inter-ocular delays* . Psychophysical studies have found that the stereoscopic
122 system can tolerate a time difference between binocularly correlated images of up to 50ms
123 (Gheorghiu & Erkelens, 2005b; Julesz & White, 1969; Ross & Hogben, 1974). As for symmetry
124 perception, which requires computation of spatially matched-elements across the symmetry
125 axis, little is known about whether symmetry mechanisms can tolerate delays between the
126 matched pairs. Only one study by Hogben et al (1976) examined the effect of temporal delays
127 between briefly presented matched-elements on *orientation discrimination* of the symmetry
128 axis and reported that symmetry perception ceased with delays of ~50-90msec. Thus, it
129 remains to be established how temporal delays between matched-elements are affected by
130 the sustained and transient stimulus presentation and by changes in the amount of symmetry
131 (i.e. strength of symmetry signals) within the temporal integration window. To test for this,
132 we will use stimuli in which symmetric pairs are presented either simultaneously or with a
133 variable time delay between spatially-matched elements. We predict that in conditions where
134 the symmetric pairs are presented with delay there will be a temporal limit beyond which the
135 symmetric elements cannot be spatially correlated. Thus, by varying the temporal delay
136 between spatially-matched elements and the amount of image symmetry over time, we will
137 examine temporal integration mechanisms for symmetry processing and their flexibility and
138 limitations (e.g. tolerance for temporal delays between spatially-matched elements).

139 Several categories of computational models have been developed for detecting and
140 localising mirror-symmetry in an image by using either pixel-by-pixel correlations between
141 the symmetric halves (Barlow & Reeves, 1979; Gurnsey, Herbert, & Kenemy, 1998; Pintsov,
142 1989), complex grouping rules (based on higher-order structural correlations) from which
143 symmetry is subsequently extracted (Labonte, Shapira, Cohen, & Faubert, 1995; Pashler,
144 1990; Wagemans, Vangool, Swinnen, & Vanhorebeek, 1993) or early spatial mechanisms such
145 as oriented filters to compute mirror-symmetry (i.e. symmetrical dot-pairs are detected
146 directly by the outputs of oriented receptive fields (RFs) of various sizes) (Cohen & Zaidi, 2013;
147 Dakin & Watt, 1994; Rainville & Kingdom, 2002). However, none of these models have
148 incorporated temporal aspects, although it is well established that RFs of cortical neurons are
149 spatiotemporally oriented, i.e. tilt along an oblique axis in the space-time domain making
150 them space-time inseparable - for a review see Orban (1991). Thus, although the existing
151 models and algorithms demonstrate that symmetry is a global image property requiring not

152 just first-order oriented filters, but additional subsequent processing (e.g. spatial correlation
153 of symmetrical pairs across the axis of symmetry) it remains to be determined what
154 consequences time (i.e. duration and synchronisation of matched-pairs) has on these models
155 and on the perception of symmetry in dynamic stimuli.

156 In this study, we examine temporal properties of symmetry perception in response to
157 *sustained and transient stimulus presentations* by using dynamic stimuli consisting of an on-
158 going alternation of two images (i.e. sustained stimulus presentation) or only two images (i.e.
159 transient stimulus presentation) containing varying amounts of symmetry about the vertical
160 axis. To investigate how spatial correlations between elements across the symmetry axis is
161 computed and integrated over time, we use patterns in which the symmetrical elements are
162 presented either simultaneously or with temporal delay. For the simultaneous (or
163 synchronous) presentation, stimuli consisted of two alternating patterns: a symmetrical
164 pattern and a noise pattern (i.e. whole patterns condition – see Fig. 1a and Movie 1 for the
165 dynamic version of the stimuli) or two patterns, each containing an equal number of
166 symmetrical pairs (i.e. matched-pairs condition - see Fig. 1b and Movie 2). To determine the
167 extent to which symmetry mechanisms tolerate delays, we used the same conditions as
168 above, but with stimulus halves and matched-pairs presented with delay i.e. delayed halves
169 (see Fig. 1c and Movie 3) and delayed matched-pairs (see Fig. 1d and Movie 4) conditions,
170 respectively. In addition, we compare symmetry perception in dynamic stimuli with that
171 obtained using static patterns resulting from temporal averaging of the two alternating
172 images (Fig. 1e). For all conditions, we varied the amount of symmetry and the temporal
173 alternation rate of the two images in order to systematically examine how the perception of
174 symmetry changes with temporal frequency. We then compare the threshold and the slope
175 of the psychometric function for the simultaneous and delayed conditions, and for both
176 sustained and transient stimulus presentation conditions. If symmetry is perceived in any of
177 the delayed conditions then this will indicate the degree to which symmetry mechanisms can
178 tolerate temporal delays between matched pairs. Altogether, these findings will provide an
179 in-depth characterisation of the temporal aspects of symmetry mechanisms in dynamic
180 stimuli and implicitly, their limitations.

181 Methods

182 *Participants*

183 Five observers participated in the sustained presentation experiment and four
184 observers in the transient presentation experiment. All participants had normal or corrected-
185 to-normal vision. Observers gave their informed consent prior to participating in the study
186 and were treated in accordance with the Helsinki Declaration (Version 6). All procedures were
187 approved by the University of Stirling, Psychology Ethics Committee.

188 *Stimuli – generation and display*

189 Stimuli were presented on a gamma-corrected 20-in ViewSonic Professional Series
190 PF817 cathode ray tube (CRT) monitor (ViewSonic, Brea, CA, USA) with spatial resolution of
191 1024x768 and refresh rate of 85Hz. A ViSaGe MKII stimulus generator (Cambridge Research
192 Systems, Cambridge, UK) in Bits# mode was used to control contrast. All stimuli were
193 presented in the centre of the monitor on a mid-grey background with mean luminance of
194 47.2 cd/m². Viewing distance was 52cm. All stimuli were generated and all data were
195 collected using PsychoPy (Peirce, 2007).

196 Stimuli were presented in a square window 9.034° in width and were comprised of 20
197 circular white dots (100% contrast) of 0.169° diameter. The symmetrical dots were positioned
198 randomly on the left side of the stimulus area and then mirrored about the vertical axis onto
199 the right side. Noise dots were positioned randomly such that equal numbers appeared in
200 each stimulus half. All dots were positioned a minimum of 0.767° apart. This resulted in a
201 stimulus dot density of 0.7 dots/deg².

202 Stimuli were dynamic dot patterns consisting of the on-going alternation of two
203 images containing different amounts of symmetry (i.e. sustained stimulus presentation) or
204 two images each presented once (i.e. transient stimulus presentation). There were five
205 temporal-arrangement conditions: (1) '*whole patterns*' consisting of a symmetrical pattern
206 alternated with a noise pattern (Fig. 1a); (2) '*delayed halves*' in which the left and right halves
207 of the symmetrical and noise patterns were presented with temporal delay (Fig. 1c); (3)
208 '*matched-pairs*' consisting of two alternating symmetrical patterns each containing equal
209 amounts of symmetrical matched-pairs (Fig. 1b). Note, this does not mean that half of the
210 dots in each image are symmetrical, but instead that half of the total number of symmetrical

211 dots in the stimulus are in each image. For example, if the stimulus contains 16 symmetrical
212 dots (i.e. eight pairs), then eight symmetrical dots (i.e. four pairs) would be shown in each
213 image; (4) '*delayed matched-pairs*' which is the same as arrangement 3, but with the
214 matched-pairs presented with temporal delay (Fig. 1d); (5) '*static*' in which the symmetrical
215 and noise elements in the two images were presented simultaneously as one static pattern,
216 which was the temporal average of the two images (Fig. 1e). Note that in both delayed
217 conditions (Fig. 1c,d) there are no matched-pairs in either time interval.

218 For each sustained condition, the two alternating images were presented for equal
219 amounts of time. For clarity, the term '*image duration*' refers to the amount of time each
220 component image of the dynamic stimulus is shown for, while the term '*total stimulus*
221 *duration*' refers to the total amount of time the dynamic stimulus (i.e. the on-going
222 alternating images) is presented on the screen for. In the sustained condition, the total
223 stimulus duration was always the same 2.35 seconds, while we varied the image duration of
224 the two alternating images between 23.5ms and 293.1ms in six steps: 23.5ms, 47.1, 58.8ms,
225 117.7ms, 235.3ms and 294.1ms. These image durations correspond to the following temporal
226 frequencies: 42.5Hz, 21.3Hz, 17Hz, 8.5Hz, 4.3Hz and 3.4Hz, respectively, and were selected to
227 ensure that, in the sustained stimulus presentation condition, they allow both alternating
228 images to be presented an even number of times within the total stimulus presentation
229 duration of 2.35 seconds.

230 In the transient presentation experiment, the individual image durations were the
231 same as those used in the sustained presentation experiment but each of the two images
232 were shown only once (i.e. for one full cycle), and as a result, the total stimulus duration (i.e.
233 image 1 and image 2 or the full cycle length) varied with the image duration. For this
234 experiment, we varied the presentation order of the two images: Image 1 followed by Image
235 2 (i.e. order 1) and Image 2 followed by Image 1 (i.e. order 2).

236 ***** Figure 1 approximately here *****

237 *Procedure*

238 A single interval forced-choice procedure was employed for both sustained and
239 transient experiments. For the sustained presentation experiment, on each trial, the stimulus
240 consisted of the ongoing alternation of two images corresponding to one of the five temporal-

241 arrangement conditions (see Fig. 1) and was presented for 2.353 secs. In the transient
242 presentation experiment, each image was only shown once in one of the two possible
243 presentation orders (i.e. order 1 or order 2). The participants' task was to indicate, by a key
244 press, whether the entire stimulus, as a whole, was symmetric or not (i.e. yes/no task). This
245 was particularly important for conditions with longer presentation times when the two
246 alternating images were perceived as flickering. In order to ensure that participants
247 understood the task they were allowed as many practice trials as necessary.

248 The amount of symmetry was varied in accordance with the method of constant
249 stimuli. For each temporal-arrangement condition and each image duration (23.5, 47.1, 58.8,
250 117.7, 235.3 and 294.1ms), we varied the percentage of symmetric dots in the stimulus
251 between 0% (noise) and 100% (fully symmetric) in steps of 5% (i.e. two dots) and measured
252 the percentage of trials in which participants perceived each stimulus as being symmetrical
253 (i.e. % perceived symmetric). In each run, corresponding to each image duration, all possible
254 levels of symmetry were presented ten times each, in random order. Each participant
255 collected a minimum of five runs for each image duration condition (550 trials) resulting in
256 3300 trials (6 image durations x 550 trials) for each temporal-arrangement condition. Given
257 the five temporal-arrangement conditions, this resulted in 16,500 trials per participant, for
258 the sustained presentation experiment. For the transient presentation experiment, a similar
259 number of trials were obtained for each presentation order condition.

260 Since the task required participants to judge whether a stimulus is symmetrical or not
261 by comparing it to an internal criterion/reference, there might be some effect of participant
262 bias. Therefore, in order to decouple sensitivity to symmetry from bias for each participant
263 and each stimulus symmetry condition, we calculated d' ("d-prime") values using the function
264 PAL_SDT_1AFC_PHFtoDP from the Palamedes toolbox (<http://www.palamedestoolbox.org>)
265 described in Kingdom and Prins (2016) and Prins and Kingdom (2009). This function converts
266 proportion hits and proportion false alarm rates into d' values for a one alternative forced-
267 choice task.

268 A logistic function was fit to the percentage 'perceived symmetric' data as a function
269 of the percentage of symmetry signal in the stimuli, for each image duration condition and
270 each temporal-arrangement condition, in order to estimate the number of symmetric dots
271 (or signal) required for the observer to perceive the dynamic pattern as symmetrical in 50%

272 of the trials. For some conditions, specifically for the delayed halves and delayed matched-
273 pairs conditions with longer image durations, participants were not able to perceive
274 symmetry, irrespective of the number of symmetrical dot-pairs present in the stimuli.
275 Therefore, for these conditions the logistic functions were very shallow and it was not possible
276 to calculate thresholds. For this reason, the slope of the logistic function (the beta β
277 coefficient) was calculated as a measure relating symmetry sensitivity and symmetry signal
278 strength: the shallower the slope (i.e. the smaller the beta coefficient), the less the participant
279 could differentiate between the different stimulus symmetry levels.

280 Results

281 *Sustained Stimulus Presentation Experiment*

282 Figure 2 shows the average across-observers sensitivity (% perceived symmetric) in
283 the symmetry perception task, as a function of the amount of symmetry in the stimulus (%
284 symmetry signal) and image duration for the whole patterns (Figure 2a), matched-pairs
285 (Figure 2b), static (Figure 2c), delayed halves (Figure 2d) and delayed matched-pairs (Figure
286 2e) conditions. For clarity, we also showed the temporal frequency (in Hz) corresponding to
287 the two alternating images (see top horizontal axis). The green areas in Figure 2 indicate
288 combinations of image duration (or temporal frequency) and percentage symmetry signal in
289 the stimulus for which the observers perceived symmetry and orange/red areas indicate that
290 no symmetry was perceived. The slope and threshold of the psychometric function
291 corresponding to each temporal-arrangement condition are shown in Figure 2f and Figure 2g,
292 respectively. Example psychometric functions for each temporal arrangement condition and
293 image duration (or temporal frequency) are shown in Figure 3 for one participant. The
294 average across-participants d-prime values corresponding to the data in Figure 2 are shown
295 in Figure 4 for each temporal arrangement condition.

296 The results in Figure 2 show that (a) for the whole-pattern condition, the percentage
297 perceived symmetric increases with image duration when symmetry signal is larger than
298 about 60% (compare lighter green areas for shorter image durations with darker green areas
299 for longer image durations in Figure 2a). This is also reflected by the slopes β and thresholds
300 of the psychometric functions fitted for each image duration (red lines in Figure 2f,g); (b) for
301 the matched-pairs condition, the percentage perceived symmetric does not change with

302 image duration (Fig. 2b) thus, both the slopes (blue lines in Figure 2f) and the thresholds (blue
303 line in Figure 2g) were comparable across image durations; (c) for both delayed halves and
304 delayed matched-pairs conditions, the percentage perceived symmetric was similar and
305 decreased gradually with image duration (Figure 2d,e), reaching the 75% level only for short
306 (<60ms) durations (dashed lines in Figure 2g). For durations longer than 60ms, symmetry was
307 hardly perceived, hence thresholds were not possible to be estimated (see dashed lines in
308 Fig.2g and also Fig.3). This is also seen in the slope of the psychometric function which
309 decreases gradually with increasing image duration (dashed lines in Figure 2f); (d) with static
310 stimuli, the percentage perceived symmetric was comparable to the whole and matched-
311 pairs conditions and, with the delayed conditions but only for short (<60ms) image durations.
312 Thus, our results indicate that symmetry detection in dynamic stimuli is processed by high-
313 pass temporal mechanisms, which are able to compute correlations across-the-symmetry-
314 midline between symmetric pairs presented with temporal delays shorter than ~60ms (i.e.
315 temporal frequencies higher than ~17Hz).

316 The d-prime results shown in Figure 4 show a similar trend to the % perceived
317 symmetric data shown Figure 2. As an indication, the average false alarm rates from which
318 these d' values were calculated were 0.23 for the whole pattern, 0.225 for the delayed halves,
319 0.212 for the matched-pairs, 0.253 for the delayed matched-pair and 0.268 for the static
320 pattern conditions. The range of d-prime values obtained in this experiment is comparable to
321 that found in previous studies that measured symmetry detection with static patterns (e.g.
322 Barlow & Reeves, 1979 $d' = 0.8 - 1.2$ approx.; Wenderoth, 1996b $= 0.85 - 1.3$ approx.).

323 A two-way repeated measures analysis of variance (ANOVA) with factors image
324 duration (23.5, 47.1, 58.8, 117.7, 235.3 and 294.1ms) and temporal arrangement (whole
325 patterns, matched-pairs, delayed halves and delayed matched-pairs) on the slope β data (Fig.
326 2f) showed a significant main effect of image duration ($F(5,20) = 9.523$, $p < 0.0001$, $\eta^2 =$
327 0.0796) and temporal arrangement ($F(3,12) = 13.65$, $p = 0.0004$, $\eta^2 = 0.1266$) and, a significant
328 interaction effect between image duration and temporal arrangement ($F(15,60) = 15.51$, $p <$
329 0.0001 , $\eta^2 = 0.2299$). Bonferroni corrected post-hoc analysis showed that all pairwise
330 comparisons between longer image durations (>60ms) in the whole pattern and the delayed
331 halves conditions were statistically significant ($p < 0.05$). Similarly, pairwise comparisons
332 between longer image durations in simultaneous and delayed matched-pairs conditions were

333 significant ($p < 0.05$). However, for the shorter image durations ($< 60\text{ms}$) none of the pairwise
334 comparisons were significant ($p > 0.05$).

335 For the threshold data (Fig. 2g), a two-way repeated measures ANOVA with factors
336 image duration and simultaneous arrangement (whole patterns vs. matched-pairs) revealed
337 no significant effect of image duration ($F(5,24) = 0.0928$, $p = 0.993$, $\eta^2 = 0.0172$), simultaneous
338 arrangement ($F(1,24) = 3.908$, $p = 0.0597$, $\eta^2 = 0.0105$), or interaction effect ($F(5,24) = 1.367$,
339 $p = 0.271$, $\eta^2 = 0.0183$). Similarly, the thresholds for the delayed-halves and delayed matched-
340 pair conditions under short image durations (dashed lines in Fig. 2g) were also not significant
341 ($p > 0.05$).

342 ***** Figure 2 approximately here *****

343 ***** Figure 3 approximately here *****

344 ***** Figure 4 approximately here *****

345 *Transient Stimulus Presentation Experiment*

346 The percentage perceived symmetric results for transient stimulus presentation are
347 shown in Figure 5 for order 1 (Figure 5a), order 2 (Figure 5b) and static (Figure 5c) conditions.
348 As with the sustained conditions, we calculated d' values for each observer and stimulus
349 symmetry condition. The average across-observers d' values are shown in Figure 6. The
350 average across-observers false alarm rates for Order 1 and Order 2 were 0.416 and 0.4158 for
351 whole patterns, 0.351 and 0.3475 for delayed halves, 0.3817 and 0.423 for matched-pairs,
352 0.3675 and 0.349 for delayed matched-pairs conditions 0.372 for the static condition. The
353 slopes of the psychometric functions corresponding to the two temporal orders are shown in
354 Figure 7. On average, these results follow a similar trend to those obtained with sustained
355 stimulus presentation (Figure 2f) but the values for the slope β are a factor of three lower,
356 reflecting overall lower sensitivity to symmetry. For the whole pattern condition at longer
357 image durations, sensitivity was slightly increased when the symmetrical image was
358 presented before the noise image (i.e. order 1 or backward masking) than vice-versa (order 2
359 or forward masking) condition – compare the first panel in Figure 5a with Figure 5b.

360 The data (slope β) for each presentation order condition were separately submitted
361 to a two-way repeated measures ANOVA, with factors image duration (23.5, 47.1, 58.8, 117.7,

235.3 and 294.1ms) and temporal arrangement (whole pattern, matched-pairs, delayed halves, delayed matched-pairs and static). The analysis revealed a significant main effect of image duration for order 2 ($F(5,15) = 4.776$, $p = 0.0082$, $\eta^2 = 0.0454$), but not order 1 ($F(5,15) = 2.074$, $p = 0.1258$, $\eta^2 = 0.0156$) conditions. The main effect of temporal arrangement was found to be statistically significant for both order 1 ($F(4,12) = 15.75$, $p = 0.0001$, $\eta^2 = 0.3217$) and order 2 ($F(4,12) = 15.45$, $p = 0.0001$, $\eta^2 = 0.3065$) conditions. The interaction effect between image duration and temporal arrangement was also significant for both order 1 ($F(20,60) = 3.558$, $p < 0.0001$, $\eta^2 = 0.09523$) and order 2 ($F(20,60) = 6.887$, $p < 0.0001$, $\eta^2 = 0.2126$) conditions. Bonferroni corrected post-hoc analysis showed a comparable pattern of statistically significant pairwise comparisons to the sustained condition with the following exceptions: in order 1, the whole pattern condition with short (23.5ms) image duration was significantly different from image durations longer than 117.7ms and, the delayed halves condition with short (23.5ms) image duration was significantly different from the synchronous conditions with longer image durations (>60ms). In order 2, the matched-pairs condition was also significantly different to the whole pattern condition with longer image durations (>60ms) and to the longest static conditions (235.3 and 294.1ms).

***** Figure 5 approximately here *****

***** Figure 6 approximately here *****

***** Figure 7 approximately here *****

381 *Comparison between transient and sustained presentations*

382 In order to determine whether sensitivity differed between the transient and
383 sustained conditions, we used a two-way repeated-measures ANOVA on the slope of the
384 linear regression line that relates the β parameter of the psychometric function to image
385 duration for each stimulus presentation type (sustained vs transient order 1 vs transient order
386 2) and temporal arrangement conditions (whole patterns, delayed halves, matched-pairs,
387 delayed matched-pairs). The analysis revealed a significant main effects of presentation type
388 ($F(3,12) = 30.73$, $p < 0.0001$, $\eta^2 = 68.38$) and temporal arrangement ($F(2,12) = 10.72$, $p =$
389 0.0021 , $\eta^2 = 15.9$). This significant difference between sustained and transient stimulus
390 presentation appears to be driven by the delayed conditions which have shallower linear

391 regression slopes in the transient than the sustained conditions. There was no significant
392 interaction between presentation type and temporal arrangement.

393 Discussion

394 We have examined symmetry perception in response to sustained and transient
395 presentations of dynamic patterns using different temporal arrangements of symmetrical and
396 random elements. Our results show that (i) with on-going, sustained presentations of
397 symmetrical and noise patterns (i.e. whole pattern condition), sensitivity increased
398 significantly for image durations longer than about 120ms; (ii) for the delayed conditions,
399 when the symmetrical pairs or halves were presented in different temporal intervals,
400 sensitivity decreased gradually with image durations longer than ~60ms suggesting that
401 symmetry detection mechanisms can tolerate time delay between positional symmetric-
402 elements of up to 60ms; (iii) for the sustained presentation of symmetric patterns containing
403 50% symmetric pairs, sensitivity was invariant with image duration when the two alternating
404 images contained equal amounts of symmetry; (iv) for the transient presentation, sensitivity
405 gradually improved as a function of image duration when the two images contained equal
406 amounts of symmetry or when they were the static, time-averaged patterns; (v) on average,
407 sensitivity was higher when the symmetric image preceded (i.e. backward masking) rather
408 than followed (i.e. forward masking) the noise pattern. Altogether, the results for the whole
409 and delayed conditions indicate that spatial-correlation across the symmetry axis can be
410 integrated over time within ~120ms time window and consequently symmetry mechanisms
411 can tolerate delays of up to 60ms.

412 Sensitivity to symmetry in the whole pattern condition increased significantly for
413 image durations longer than 120ms (see green areas in Fig.4a and 6a) suggesting that
414 symmetry detection mechanisms integrate symmetric and noise patterns within a time
415 window of ~120 ms. For sustained stimulus presentation, we found comparable sensitivity to
416 symmetry between *simultaneous* and *delayed* image conditions up to about 60ms image
417 duration (see green areas in Fig. 2d and also thresholds in Fig. 2g), suggesting that symmetry
418 detection mechanisms can compute spatial correlations between temporally delayed
419 matched dot-pairs and/or between symmetric halves of up to 60ms. This tolerance for
420 temporal delays of up to 60ms is a consequence of a temporal integration process occurring
421 within 120ms. The present results show that the computation of spatial correlations across-

422 the-symmetry-midline *over time* is limited to about 17Hz alternation frequency, suggesting
423 that symmetry detection in *dynamic stimuli* is processed by a relatively high-pass temporal
424 mechanism.

425 In our experiments, we found increased sensitivity with sustained compared to
426 transient stimulus presentations suggesting that symmetry mechanisms integrate
427 simultaneously presented matched-pairs over time. Overall, the slopes β of the psychometric
428 function for the transient conditions were about three times lower than for the sustained
429 presentation conditions (compare Figure 2f and Figure 7). Additionally, the slopes of the linear
430 regression lines are shallower for sustained presentation compared to transient presentation,
431 suggesting that sensitivity decreases more rapidly with image duration when presentation is
432 transient. This lower sensitivity with transient stimuli comes at odds with previous literature
433 showing that symmetry can be reliably perceived in very briefly presented stimuli of under
434 50ms (Julesz, 1971; Tyler et al., 1995). However, a number of studies have shown that even
435 with fully symmetric patterns (100% symmetry signal), performance never reached 100%
436 correct detection but remains limited to ~80% correct detection (Tyler et al., 1995;
437 Wenderoth, 1996a). For the *whole patterns* in the transient presentation condition, sensitivity
438 to symmetry was affected by the presentation order of the symmetric and noise patterns,
439 with significantly lower sensitivity for shorter image durations (less than 60ms) when the
440 symmetrical pattern was presented before the noise pattern (i.e. backward masking). This is
441 similar to findings from depth perception studies where with transient stimulus presentations
442 the perception of stereoscopic depth was affected by the presentation order of correlated
443 and uncorrelated random dot images (Gheorghiu & Erkelens, 2004).

444 Our results showing that symmetry can be perceived in delayed halves and delayed
445 matched-pairs conditions for very short image durations (<60ms), despite there being no
446 symmetrical matched-pairs in either time interval, suggest that symmetry detection
447 mechanisms can compute spatial correlation across the symmetry axis between matched
448 pairs presented with short delays and integrate these weak symmetry signals over a time
449 period of ~120ms. The tolerance to delays between presentations of matched-pairs up to
450 ~60ms found in the current study is in keeping with previous findings by Niimi et al. (2005)
451 who reported that symmetry can be detected in briefly-presented split symmetric-halves
452 presented with a stimulus onset asynchrony (SOA) of 87ms. These authors explained their

453 results in terms of visual persistence (i.e. a briefly presented stimulus outlasts its physical
454 presentation on the screen) or visual memory (Di Lollo, 1980; Niimi et al., 2005) given that
455 the images were briefly flashed for 13ms. However, by using a variable stimulus onset
456 asynchrony (SOA), the strength of briefly presented symmetry signals may decay over time at
457 different rates depending on image duration, and one cannot define temporal frequency for
458 unequal combinations of image durations and SOAs.

459 Altogether our sustained and transient presentation results suggest that symmetry
460 mechanisms can integrate weak symmetry signals over a time period of 120ms. The lower
461 sensitivity with transient compared to sustained stimulus presentations could be explained
462 by the presence of a weaker, transient symmetry signal within the temporal integration
463 period than when the symmetry signals are presented in an ongoing manner. This is in
464 keeping with previous findings from Cohen and Zaidi (2013) showing the temporal thresholds
465 for detecting the orientation of the axis of symmetry in natural textures varied broadly,
466 suggesting a wide range of stimulus salience which was quantified by the inverse of the
467 temporal threshold (i.e. $1/\text{threshold}$).

468 Recently, Cohen and Zaidi (2013) have proposed a model for estimating symmetry-
469 energy in natural textures by connecting pairs of symmetric spatial filters simulating the RFs
470 of neurons. If the two orientations were related by mirror-symmetry, then an AND junction
471 was activated. If the outputs of the two filters were about equal then they were summed into
472 a symmetry-energy index which accurately identified the spatial position of the axis of
473 symmetry for most stimuli but correlated poorly with the stimulus salience (i.e. $1/\text{temporal-}$
474 threshold). Thus, it remains unclear what consequences time (i.e. duration and
475 synchronisation of symmetric pairs) has on this model as well as on other models of symmetry
476 detection based on spatial oriented filters (Dakin & Watt, 1994; Rainville & Kingdom, 2002).
477 However, our findings suggest that the current models of symmetry detection (e.g. the AND-
478 gating model of Cohen & Zaidi, 2013) must include computations of spatial correlations
479 between the outputs of spatiotemporal oriented filters that integrate symmetry information
480 within $\sim 120\text{ms}$. If the outputs of the two filters are delayed longer than 60ms then the AND-
481 gate will not be activated and symmetry will not be perceived.

482 Due to the long overall stimulus duration in the sustained presentation experiment
483 (2.35 sec) one might think that eye movements could contribute to symmetry detection

484 (Meso, Montagnini, Bell, & Masson, 2016). Meso et al. (2016) reported that eye movements
485 made by observers viewing static symmetric stimuli generated more saccades parallel to the
486 axis of symmetry than along other orientations, and this observed parallel orientation-
487 selectivity emerged within 500ms of stimulus onset. Although our sustained stimulus
488 presentation was 2.35 sec, it is unlikely that eye movements contributed to our results as
489 each image was only presented briefly, for between 23.5 and 294.1 ms. These image
490 durations are shorter than the time needed to plan eye movements (<180-200 ms) (Collewinj,
491 Erkelens, & Steinman, 1997) and/or scan the images (Meso et al., 2016).

492 *Relationship with electrophysiological and neurophysiological studies*

493 A number of studies examined the time course of neuronal responses to symmetry
494 perception by measuring event related potentials (ERP) in response to symmetric and quasi-
495 random patterns (Bertamini & Makin, 2014). These studies found that the amplitude in
496 posterior electrodes is comparable for symmetric and quasi-random patterns up to 200ms
497 after stimulus onset. After that time (i.e. 200-600ms) the amplitude becomes lower for
498 symmetric than quasi-random patterns, resulting in a difference-wave termed the Sustained
499 Posterior Negativity (SPN) (Bertamini & Makin, 2014; Norcia, Candy, Pettet, Vildavski, & Tyler,
500 2002). These studies suggest that symmetry is extracted relatively late, after non-symmetric
501 specific form processing (Norcia et al., 2002). The current work does not address the time
502 course of neuronal/ electrophysiological responses to symmetric stimuli but rather examined
503 the temporal properties of symmetry perception by considering how temporal
504 synchrony/asynchrony between matched pairs and image duration affect the integration of
505 perceptual grouping of symmetrical elements across the vertical axis over time. This differs
506 from ERP findings, as the SPN is not necessarily related to symmetry per se, but rather
507 structure or regularity in a stimulus (Bertamini & Makin, 2014) and, therefore, may not reflect
508 the temporal accumulation or integration process required to perceive symmetry.

509 Neuro-imaging studies have shown that symmetry generates a distinctive pattern of
510 brain activity over a wide network of extra-striate areas (Bertamini & Makin, 2014; Sasaki et
511 al., 2005; Tyler et al., 2005). To our knowledge, there are no neurophysiological studies of
512 symmetry perception in neurons sensitive to symmetry. Although brain imaging studies found
513 that there is no differential activation in areas V1 and V2 for symmetrical versus asymmetrical
514 stimuli (Cattaneo, Mattavelli, Papagno, Herbert, & Silvanto, 2011; Chen, Kao, & Tyler, 2007;

515 Sasaki et al., 2005), there is some neurophysiological evidence that V1 neurons exhibit
516 enhanced responses at the medial (symmetry) axis of simple geometric figures defined by
517 texture, about 80ms after stimulus onset (Lee, Mumford, Romero, & Lamme, 1998). However,
518 it is unclear what the consequences of temporal delays are for neurons exhibiting sensitivity
519 to the medial axis of symmetry. It is known that symmetry is poor in the periphery (Gurnsey
520 et al., 1998) and perception is focused around the axis of symmetry with the exact size of the
521 *spatial* integration window determined by the size of pattern elements (Rainville & Kingdom,
522 2002). However, direct neurophysiological research is needed to understand the dynamics of
523 symmetry mechanisms at neuronal level.

524 To conclude, we showed that observers' sensitivity to symmetry was higher for
525 sustained compared to transient presentations and when symmetrical pairs were presented
526 simultaneously rather than with temporal delay. Overall, we found (a) comparable
527 sensitivities between simultaneous and delayed conditions up to about 60ms per image
528 suggesting that symmetry signals are integrated over a time period of ~120 ms. (b) a gradual
529 decrease in sensitivity in the delayed conditions for longer (>60 ms) image durations. We
530 conclude that spatial correlation between matched-pairs (and/or stimulus halves) across the
531 symmetry axis can be integrated over time and symmetry detection mechanisms can tolerate
532 temporal delays between symmetrical pairs of up to approximately 60ms.

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674

675 [Supplementary material](#)

676 All data and analyses are available online at <http://hdl.handle.net/11667/95>.

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680 [Authors Contributions](#)

681 Conceived and designed the experiments: RJS, EG. Performed the experiments: RJS,
682 SG. Analysed the data: RJS, SG. Wrote the paper: RJS, EG.

683 [Competing Interests](#)

684 The authors declare no competing interests.

685 [Figure Legends](#)

686 **Figure 1.** Example stimuli. Symmetrical (signal) dots are outlined in green, with matched pairs having the same
687 shaped outline (i.e. circle or square). Random (noise) dots are outlined in red. Red and green outlines are for
688 illustrative purposes and not present in the actual stimuli. There were five temporal-arrangement conditions:
689 (a) ‘Whole patterns’ in which a symmetrical pattern (Image 1) is alternated with a noise pattern (Image 2). (b)
690 ‘Matched-pairs’ – half of the total number of symmetrical dots are presented in each image or interval (see
691 green circles and squares). (c) ‘Delayed halves’ in which left and right halves of the symmetrical and noise
692 patterns were presented with temporal delay, i.e. half of the symmetrical pattern is presented in each image or
693 interval. (d) ‘Delayed matched-pairs’ – delayed version of (c), i.e. the matched elements are presented in
694 different intervals as shown by the green squares and circles. Note that in both delayed conditions (c) and (d)
695 there are no symmetrical matched-pairs in either time interval. (e) ‘Static’ in which the symmetrical and noise

696 elements in the two images were presented simultaneously as one single static pattern which was the time
697 average of Image 1 and Image 2.

698 **Figure 2. Sustained stimulus presentation experiment.** The average across-observers percentage perceived
699 symmetric as a function of the amount of stimulus symmetry (% symmetry signal) and image duration for (a) the
700 whole patterns, (b) matched-pairs, (c) static, (d) delayed halves and (e) delayed matched-pairs stimulus
701 conditions. For clarity, we also show the temporal frequency (in Hz) corresponding to the two alternating images
702 (see top horizontal axis). The colour bar/ key (below) shows the colours corresponding to each percentage
703 perceived symmetric. The line graphs show averaged across-participants (f) slopes and (g) thresholds of the
704 psychometric function for the whole patterns (red solid line), delayed halves (red dashed line), matched-pairs
705 (blue solid line), delayed matched-pairs (blue dashed line) and static (green line). Errors bars and the green band
706 for the static condition are +/- 1 SEM.

707 **Figure 3. Example psychometric functions fitted to the % perceived symmetric data for one participant in the**
708 **sustained stimulus presentation experiment.** Logistic psychometric functions for the whole patterns (red solid
709 line), delayed halves (red dashed line), matched-pairs (blue solid line), delayed matched-pairs (blue dashed line)
710 and static (green line) conditions for each of the six image durations tested.

711 **Figure 4. D-prime (d') values for the sustained stimulus presentation experiment.** The average across-observers
712 d' values for each amount of stimulus symmetry (% symmetry signal) and image duration/temporal frequency
713 for (a) the whole patterns, (b) matched-pairs, (c) static, (d) delayed halves and (e) delayed matched-pairs
714 stimulus conditions. The colour bar/ key (below) shows the colours corresponding to each d' value.

715 **Figure 5. Transient stimulus presentation experiment.** The average across-observers percentage perceived
716 symmetric as a function of the amount of stimulus symmetry (% symmetry signal) and image duration for (a)
717 Order 1 – Image 1 followed by Image 2, (b) Order 2 – Image 2 followed by Image 1 and, (c) static conditions. The
718 left-to-right panels indicate the results for the whole patterns, matched-pairs, delayed halves and delayed
719 matched-pairs conditions respectively. The horizontal colour bar at the bottom shows the colours corresponding
720 to each percentage perceived symmetric.

721 **Figure 6. D-prime (d') for transient stimulus presentation experiment.** The average across-observers d' values
722 for each amount of stimulus symmetry (% symmetry signal) and image durations for (a) Order 1 – Image 1
723 followed by Image 2, (b) Order 2 – Image 2 followed by Image 1 and, (c) static conditions. The left-to-right panels
724 indicate the results for the whole patterns, matched-pairs, delayed halves and delayed matched-pairs conditions
725 respectively. The horizontal colour bar at the bottom shows the colours corresponding to each d' value.

726 **Figure 7. Slopes of the psychometric functions for the transient stimulus presentation experiment.** The line
727 graphs show the averaged across-participants slopes β as a function of image duration for (a) Order 1 and (b)
728 Order 2 for the whole image (red solid line), delayed halves (red dashed line), matched pairs (blue solid line),
729 delayed matched pairs (blue dashed line) and static (green line). Errors bars are +/- 1 SEM.

730