Temporal processing characteristics of the Ponzo illusion

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Abstract

Many visual illusions result from assumptions of our visual system that are based on its longterm adaptation to our visual environment. Thus, visual illusions provide the opportunity to identify and learn about these fundamental assumptions. In this paper, we investigate the Ponzo illusion. Although many previous studies researched visual processing of the Ponzo illusion, only very few considered temporal processing aspects. However, it is well known that our visual percept is modulated by temporal factors. First, we used the Ponzo illusion as prime in a response priming task to test whether it modulates subsequent responses to the longer (or shorter) of two target bars. Second, we used the same stimuli in a perceptual task to test whether the Ponzo illusion is effective for very short presentation times (12 ms). We observed considerable priming effects that were of similar magnitude as those of a control condition. Moreover, the variations in the priming effects as a function of prime-target stimulus-onset asynchrony were very similar to that of the control condition. However, when analyzing priming effects as a function of participants' response speed, effects for the Ponzo illusion increased in slower responses. We conclude that although the illusion is established rapidly within the visual system, the full integration of context information is based on more time-consuming and later visual processing.

Keywords: Visual illusions, Ponzo illusion, time course, temporal development, response priming

Introduction

Visual illusions: a window to our brain

A visual illusion occurs when the physical characteristics of a given stimulus do not match the visual percept of observers. Many illusions result from assumptions of our visual system that are based on its long-term adaptation to our visual environment (e.g., Howe & Purves, 2004, 2005a, 2005b). These adaptations cause stereotypical and sometimes inappropriate interpretations of visual scenes. Consequently, understanding these illusions means to unravel the perceptual and neuronal mechanisms by which our subjective percept is created from the retinal image. In other words, bv investigating visual illusions it is possible to reveal fundamental principles of visual processing (Eagleman, 2001; Gregory, 2005; Palmer, 1999).

Here, we focus on the Ponzo illusion (Ponzo, 1911), in which two identical lines appear to be of different size when placed over different sections of converging context lines (Figure 1, left panel). Thereby, the illusion exemplifies the fundamental dependency of our judgments about object size on context. More specifically, because the two red bars are placed within a context that might suggest that both are located at different distances (Gregory, 1966), the "far" bar might appear to be larger than the "near" bar. This principle can be further demonstrated by placing two identical figures in a real-world scene with linear perspective (Figure 1, right panel). Thus, the Ponzo illusion might illustrate that depth cues that are presented within twodimensional images may set constancy scaling inappropriately.

In the present study, we investigate the time course of processing of the Ponzo illusion. But why is it generally important to know the time course of visual perception processes?

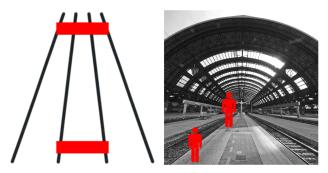


Figure 1. Illustration of the Ponzo illusion. Classical Ponzo illusion, in which the size of two identical bars appears different depending on context (left panel). Ponzo illusion in a real-world context, in which the size of two identical figures superimposed on a photo of Milan central station appears different because of their perceived distance (right panel). Photo copyright 2011 by John Picken. Reprinted with permission.

The time course of visual perception

The perceptual representation of our environment is built up through successive stages of perceptual formation unfolding within the first few hundred milliseconds after stimulus presentation. This was demonstrated early on by showing that our percept develops on a brief present-time scale (microgenesis; cf. Bachmann, 2006). This idea of the formation of microgenetic stable representations with its long research tradition fits well the increasing number of modern theories of visual perception which stress the aspects of visual temporal processing. Typically, these theories emphasize the difference between (1) a temporally early phase of processing - mediated by neuronal feedforward activation, and (2) a later phase of processing - mediated by recurrent activation, that is, neuronal feedback between higher and lower levels of the visual hierarchy and lateral/horizontal connections within levels (e.g., Bullier, 2001; Hochstein & Ahissar, 2002; Lamme & Roelfsema, 2000; Roelfsema, 2006; Schmidt, Haberkamp, Veltkamp et al., 2011).

This distinction between early and late phases of processing is crucial because the recurrent processing in the late phase is a necessary precondition for many aspects of visual perception (e.g., *figure-ground segmentation*, Zhou, Friedman, & von der Heydt, 2000; or *visual awareness*, Lamme, 2006). This implies that our visual percept might be qualitatively different between temporally early and late processing phases. Indeed, as already demonstrated in previous microgenetic research (e.g., Werner, 1957), our visual percept changes rapidly in time. Importantly, the nature of these changes promises to provide valuable information cognitive and about the physiological underlvina respective mechanisms а perceptual process (for recent reviews see Hegdé, 2008; Ögmen & Breitmeyer, 2006; van Zoest, Hunt, & Kingstone, 2010).

The time course of the Ponzo illusion

This change in the visual percept over time has also been observed in visual illusions, traditionally by using the method of tachistoscopic presentation in which the effect of an illusion is measured as a function of its presentation time (e.g., Piaget, 1961). What can the time course of visual illusions tell us about visual perception in general?

Changes in the illusory percept provide information about the respective principle of visual perception inducing the illusion. These principles might be effective early on, or only implemented in the context of later and more elaborate representations that are based on recurrent processing. For example, the integration of information across space that is also necessary to integrate bars and context in the perception of the Ponzo illusion (Figure 1) might be mediated by different recurrent mechanisms: either by horizontal connections within levels of the visual hierarchy, by the increasing receptive field sizes at higher levels, or by modulatory feedback from these. In line with the latter notion, some authors argue that the Ponzo illusion is likely based on feedback projections from higher visual areas which extract the three-dimensional context of the background (Schwarzkopf, Song, & Rees, 2010; Song, Schwarzkopf, & Rees, 2011). From this would follow that the Ponzo illusion should not be (very) effective in early, processing. feedforward phases of An influence of the Ponzo illusion on rapid visuomotor priming effects - that have linked previously been to feedforward Schmidt, Haberkamp. processes (e.g., Veltkamp et al., 2011) - would put serious constraints on this assumption.

Earlier studies on the time course of the Ponzo illusion produced equivocal results. For example, Oyama and Morikawa (1985) presented participants with the Ponzo illusion for either 25 ms or 1000 ms and did not find a difference in the strength of the illusory percept in a perceptual staircase measure. The authors conclude that the Ponzo illusion reaches its maximum within only 25 ms. In a similar paradigm, Reynolds (1978) presented participants with the Ponzo illusion for 50 ms, followed by a mask with SOAs (stimulus-onset asynchrony) of 50, 75, 100, 150, 200, and 250 ms. In contrast to the results of Oyama and Morikawa (1985), his findings suggest that the Ponzo illusion is developing over the course of the first 300 ms after stimulus presentation: there is only a weak illusory percept for SOAs < 150 ms, and the maximum is not reached before SOA = 250 ms. Somewhat similar results were obtained by Luccio (1969) who presented participants with the Ponzo illusion for either 10, 20, 40, or 500 ms. The results show that the illusion is increasing with presentation time, reaching its maximum between 20 and 40 ms, and then for 500 ms decreasing again to a magnitude similar to that obtained for 10 ms.

In although results sum. are pointing heterogeneous, thev are to quantitative changes in the illusory percept over the time course of processing. This is also supported by a more recent study that reported illusory effects on response times when presenting a variant of the Ponzo illusion for 40 ms but no effects when presenting it for a shorter time (Plewan, Weidner, & Fink, 2012). Note that the authors of the study conclude from their results that the integration of distance information with other sources of information takes at least 40 ms.

In the current study, we investigate the time course of the Ponzo illusion by indirect response time measures (response priming) and compare these results to a perceptual with same stimuli measure the and experimental surroundings. Response priming is especially useful in measuring the early time course of visual processing and can potentially dissociate between temporally early and late processing phases in visual perception (cf. Schmidt, Haberkamp, Veltkamp et al., 2011).

Response priming as a tool to investigate the time course of processing

Most of the studies discussed until now did either vary the presentation time or the SOA between the illusion and a subsequent mask and measured the effect on the illusory percept. Only few studies investigated the role of illusions on response times (e.g., on saccade latency, de Brouwer, Brenner, Medendorp, & Smeets, 2014; van Zoest & Hunt, 2011). Here, we use a response priming paradigm (Klotz & Neumann, 1999; Klotz & Wolff, 1995; Schmidt, Haberkamp, & Schmidt, 2011; Vorberg, Mattler, Heinecke, Schmidt, & Schwarzbach, 2003) that is suited to investigate the influence of visual (prime) stimuli fast visuomotor processing. on Participants perform speeded responses to target stimuli which are preceded by prime stimuli mapped either to the same response as the targets (consistent primes) or to the alternative response (inconsistent primes). Consistent primes speed responses to the targets whereas inconsistent primes slow responses, and this response priming effect (i.e. the difference between consistent and inconsistent trials) increases with prime-target SOA at a rate depending on the strength of the prime signal (e.g., its color contrast; Schmidt, Niehaus, & Nagel, 2006; Vath & Schmidt, 2007). Generally, response priming effects occur because the prime activates the response assigned to it. This has been shown early on in the time course of lateralized readiness potentials (e.g., Klotz, Heumann, Ansorge, & Neumann, 2007) as well as in online measurements of pointing or force responses (e.g., Schmidt et al., 2006; Schmidt, Weber, & Schmidt, 2014). Response priming has not only been demonstrated for basic features like color or shape, but also for complex figural features like closure and (Schmidt & Schmidt. symmetry 2013). However, in the case of complex features, priming effects are diminished and do often only reach their full magnitude with longer SOAs and in slower responses. Thus, the time course of visual processes can be investigated by looking at the magnitude of response priming effects as a function of SOA and response speed - because both leave the visual system with more time to process the stimuli.

Finally, the response priming task can potentially dissociate between temporally early and late processing phases in visual perception. These dissociations can be revealed by comparing results for specific stimuli in a perceptual task to results of the same stimuli in a priming task. For example, the effects of masked primes can be dramatically different in perception and visuomotor priming: invisible primes can produce large response priming effects (e.g., Kiesel, Kunde, Pohl, Berner, & Hoffmann, 2009; Vorberg et al., 2003). A similar dissociation was reported for brightness processing (Schmidt et al.. 2010). dissociations Demonstrating between perception and priming would be especially interesting in visual illusions that incarnate fundamental principles of visual processing. Indeed, we have demonstrated this type of dissociation for the Ebbinghaus and Delboeuf illusion (e.g., Weber, Noé, Hoffmann, Schmidt, & Schmidt, 2012).

We use a primed flanker task, a variant of the response priming paradigm (Schmidt & Schmidt, 2013), in which participants respond to the size of two targets (Figure 2). Preceding primes are either physically the same as the produce targets and should standard response priming effects, or they are Ponzo stimuli that should induce priming effects only when the illusion is effective for shortly presented primes. The results of the standard priming task act as a control condition. Finally, we test the magnitude of the illusion in a traditional, perceptual task with the same stimuli and experimental surroundings. This perceptual task is as similar as possible to the primina task to allow for meaningful conclusions from a potential dissociation between the results in both tasks (Schmidt & Vorberg, 2006). It also represents the method of forced choice discrimination which is an established method to measure the perceptual strength of visual illusions (e.g., Doherty, Campbell, Tsuji, & Phillips, 2010; Moore & Egeth, 1997; Reynolds, 1978).

In case the Ponzo illusion is based on feedforward processing, it should produce priming effects already in short SOAs and in fast responses that do not increase in longer SOAs and slower responses. In case the Ponzo illusion is based on slower, recurrent processing, it should produce either no priming effects or effects that increase in longer SOAs (compared to the standard response priming effects) and in slower responses.

At the same time, we can investigate whether the Ponzo illusion has some temporal maximum (cf. Piaget & Matalon, 1958) in its influence on visuomotor processing. Because prime presentation time is only 12 ms, priming effects would also provide counter-evidence with respect to the previously reported minimum of 40 ms presentation time (Plewan et al., 2012).

Experiment

In the primed flanker task a pair of primes at the center of the screen is succeeded by a pair of targets flanking the primes (Figure 2; cf. Schmidt & Schmidt, 2013, 2014; Schmidt, Weber, & Schmidt, 2014). This task has several advantages. First, the response to the relevant stimulus dimension (e.g., size) is based on the comparison of two stimuli (twoalternative forced-choice task, 2AFC task). This makes the task easier and allows for faster responses. Second, targets do not cover the same positions as the primes. This precludes masking and temporal integration effects. Importantly, because response priming works irrespective of whether primes are presented at identical or separate positions from the targets (Vorberg et al., 2003), the results of the task can be compared to earlier findings with non-flanker paradigms.

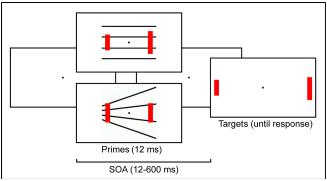


Figure 2. Stimuli and procedure. Primes and flanking targets were presented in the sequence displayed. Participants responded to the length of the red target bars by pressing a left or right button depending on which side of the display the longer (or shorter respectively) bar appeared. Prime bars in the color of the targets were either of the same lengths as targets and presented against a

background of horizontal black lines (control stimuli, upper panel) or of the average target length and presented against a background of converging black lines (Ponzo stimuli, lower panel). Primes and targets were either consistent with respect to the position of the physically (control stimuli) or perceived (Ponzo stimuli) longer (shorter) bar (here: primes upper panel), or inconsistent (here: primes lower panel). Thus, Ponzo stimuli will only induce priming effects when the illusion is effective.

Methods

Participants. Eight students from the University of Kaiserslautern, Germany (4 female, 4 male, ages 20-29), with normal or corrected vision participated in the experiment. All participants provided written informed consent in accordance with the Declaration of Helsinki and were treated in accordance with the ethical guidelines of the American Psychological Association. They were debriefed after the final session.

Apparatus and Stimuli. The participants were seated in a dimly lit room in front of a CRT color monitor (1280 x 1024 pixels) with a monitor retrace rate of 85 Hz at a viewing distance of approximately 70 cm. They responded with their left and right index fingers standard keyboard. Stimulus via а presentation and timing was controlled by using Presentation® software (www.neurobs.com). Timing uncertainties were generally smaller than 0.2 ms and different conditions did not lead to differences in the performance of the program.

For the priming task, all stimuli included red bars of 0.65° width (10 mm \approx 0.82° of visual angle) and different lengths. Targets were either long (3.27°) or short (2.29°) bars. Primes were two combinations of bars and background lines: control stimuli or Ponzo stimuli. Control stimuli were bars of the same size as the targets presented against a background of four horizontal black lines (0.16° x 8.02°). Ponzo stimuli were bars of the average target length (2.78°) and presented against a background of four converging black lines (outer lines: 0.16° x 8.43°; inner lines: $0.16^{\circ} \times 8.10^{\circ}$). The length of the bars were initially chosen based on judgments of lab members such that the perceived difference

was similar between bars in control and Ponzo stimuli. Within the experiment, we measured this perceived difference in a perceptual task.

Primes and targets were presented on the left and right of a fixation square $(0.08^{\circ} \times 0.08^{\circ})$. The center-to-center distance between fixation and targets was 5.65°, that between fixation and primes was 4.01°. All stimuli were presented in black (0.13 cd/m^2) and red (44.20 cd/m²) against a white background (60.00 cd/m²). Fixation remained on screen at all times.

For the perceptual task, stimuli were combinations of bars and background lines. Red bars were either of the same length (2.78°) or of different length and presented against a background of four horizontal black lines (control stimuli) or four converging black lines (Ponzo stimuli). The different lengths were obtained by step-wise shortening one of the bars of the same length by ~0.05° and lengthening the other by $\sim 0.05^{\circ}$. In that way, we produced 18 pairs of bars with different length. The pair with the largest difference was 1.90° and 3.66°. The pairs also included one pair exactly as long as the targets in the priming task (i.e., 2.29° and 3.27°). We combined these 19 (including the same) bar lengths with the background of (1) four horizontal lines – 19 control stimuli, or (2) four converging lines in a way that the change in length either contradicted the illusion (i.e., the shorter bar on the side of the convergence point) or supported the illusion (i.e., the longer bar on the side of the convergence point) -38Ponzo stimuli. The spatial arrangement of these stimuli was the same as in the priming task, only that there were no target stimuli presented.

Procedure: Priming task. This task was designed to measure the effect of the Ponzo illusion on rapid visuomotor processing. Each trial showed two peripheral targets, preceded by two central primes at varying prime-target SOAs (Figure 2). The task of the participants was to indicate as quickly and accurately as possible on which side of the display the target bar was longer (half of participants: shorter) by pressing a left or right button. Primes and targets were either consistent or inconsistent with respect to the required response. Specifically, for control stimuli, the longer bar was on the side of the longer target (consistent) or on that of the shorter target (inconsistent). For Ponzo stimuli, the black lines converged on the side of the longer target (consistent, because the Ponzo illusion should prolong the bar on that side) or on that of the shorter target (inconsistent). Participants were asked to focus on fixation at all times.

Primes were presented for 12 ms and targets were presented until participants' response. The time interval from fixation to target onset was constant at 1000 ms to allow for preparation to the target. To measure the time course of the effect, the SOA was varied in 10 steps over a wide range between 12 and 600 ms (12, 36, 60, 84, 108, 130, 248, 365, 482, 600 ms). To avoid systematical biases in response criteria. participants' we administered short SOAs ≤ 108 ms and long SOAs > 108 ms in two separate sessions (see Schmidt, Haberkamp, & Schmidt, 2011). Every session contained a practice block, followed by 35 blocks of 40 trials each. Summary feedback on response times and error rates was provided after each block. After the two sessions of the priming task, participants performed one session of the perceptual task.

Procedure: Perceptual task. This task was designed to directly measure the perceptual effect of the illusion, given the same stimuli and stimulus durations as in the priming task. This is important because the perceptual effects of illusions are susceptible to the method of measurement (Foster & Franz, 2014). Each trial showed a central stimulus equivalent to the prime stimuli without flanking targets. The stimulus was picked randomly from the 19 control stimuli and the 38 Ponzo stimuli. The task of the participants was to indicate on which side of the display the bar appeared longer (half of participants: shorter) by pressing a left or right button. There was no time limit. Participants were asked to focus on fixation at all times.

Stimuli were presented for 12 ms. A practice block was followed by 19 blocks of 40 trials each. Each participant responded 10 times to each control stimulus and to each Ponzo stimulus in which the change in length supported the illusion, as well as 20 times to each Ponzo stimulus in which the change

contradicted the illusion. Because we were interested in the subjective percept of participants, no feedback was provided.

treatment and statistical Data methods. In the priming task, the trials of the practice blocks and those with response times shorter than 100 ms or longer than 1000 ms were not analyzed. Those cut-off criteria eliminated 0.22% of trials. We performed repeated-measures analyses of variance (ANOVAs) for response times and error with factors of consistency (C), prime-target SOA (S), and prime stimulus (P). Note that the priming effect is defined as the difference between mean response times or error rates in consistent compared to inconsistent trials and is therefore characterized by the factor consistency.

To analyze the time course of responses in more detail, we looked at the response time distributions. We vincentized raw response times (full distribution without any setting of cut-off criteria) by sorting them into multiple ordinal bins of data (Ratcliff, 1979). Each bin summarized 10% of the cumulative distribution, starting from the fastest response times all the way through the slowest ones. We did this sorting separately for each participant and condition (defined by the levels of consistency and SOA, separately for control and Ponzo stimuli). As a result, the priming effect can be examined as a function of SOA and response speed. The last bin was excluded because it is likely to be distorted by outliers. ANOVAs were calculated separately for each level of SOA and included the new factor of bin (B).

In the perceptual task, the trials of the practice block were also not analyzed. Participants responses were analyzed with respect to the physical difference between the two bars in the control and Ponzo stimuli. We collapsed responses across participants and Ponzo stimuli and compared the point of subjective equality between control and Ponzo stimuli.

All p values are Huynh-Feldt-corrected and F values are reported with subscripts indicating the respective effect (e.g., F_{CxS} for the interaction of consistency and prime-target SOA). All error rates were arcsine-transformed to comply with ANOVA requirements. Additionally, we report the effect size η^2 (cf. Levine & Hullet, 2002). Note that according to Cohen (1988) an effect size (η^2) of 0.01 reflects a small, of 0.059 a medium, and of 0.138 a large effect.

Results and Discussion

We first describe the results of the perceptual task that measured the participants' percept of our stimuli, and then the influence of this percept on visuomotor responses as measured in the priming task.

Perceptual task. The results for each type of stimuli are displayed in Figure 3. For control stimuli, participants performed at chance level when bars were about equal length and were increasingly better at estimating relative length with increasing difference between bars. This pattern of results is dramatically different for the Ponzo stimuli where participants performed at chance level when bars were different by about 30%. Note that the variations in the lengths of the red bars is the same in all stimuli - the performance differences do solely result from the different arrangements of the four black lines in the background.

For statistical comparison, we fitted logistic functions for each participant. The estimated points of subjective equality were clearly different between control and Ponzo stimuli [T(7) = 12.72, p < .001], validating the perceptual effect of the illusion. The total difference in the length of the bars that was abolished by the illusion was about 0.78° (short bar: 2.39° vs. long bar: 3.17°), and thereby similar to the physical difference between the actual target bars that was about 0.98° (short bar: 2.29° vs. long bar: 3.27°). This pronounced effect of the illusion was obtained although stimuli were displayed for only 12 ms.

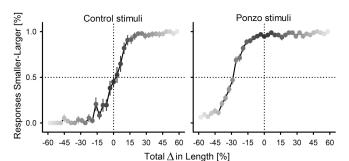


Figure 3. Results of the perceptual task for control stimuli (left panel) and Ponzo stimuli (right panel). Each panel displays percent smaller-larger responses as a function of the physical difference between the two bars with respect to their equal length of 2.78° (e.g., a total difference of 15% is defined by a 7.5% increase in the length of one bar and a corresponding 7.5% decrease in the length of the other bar). The horizontal dotted line indicates chance performance, the vertical dotted line the point of physical equality of both bars. Error bars denote the standard error of the mean.

Priming task: Response times and error rates. The results for control and Ponzo stimuli are displayed in Figure 4. For control stimuli, a 2 (C) x 10 (S) ANOVA showed regular response priming effects: response times were faster $[F_C(1,7) = 51.64, p < .001, n^2$ = 0.251 and error rates lower [F_c(1,7) = 12.42, p = .010, $\eta^2 = 0.267$ in consistent compared to inconsistent trials. These effects increased with SOAs up to 130 ms and started to decrease again with SOAs larger than 248 ms in response times $[F_{CxS}(9,63) = 11.41, p <$ $.001, \eta^2 = 0.166$ and error rates [F_{CxS}(9,63) = 8.49, p < .001, η^2 = 0.195]. Priming effects in response times were present in all participants $[p_{C} < .008;$ error rates: in 7 participants, $p_{C} <$.035], and decreased with SOA in 7 participants [p_{CxS} < .001; error rates: in 4 participants, $p_{CxS} < .001$].

Interestingly, this time course of priming was very similar for Ponzo stimuli. In a 2 (*C*) x 10 (*S*) ANOVA, priming effects in response times [$F_C(1,7) = 59.94$, p < .001, $\eta^2 = 0.317$] and error rates [$F_C(1,7) = 22.44$, p = .002, $\eta^2 = 0.338$] increased significantly with SOAs up to 108 ms and started to decrease again with SOAs larger than 130 ms in response times [$F_{CxS}(9,63) = 6.52$, p = .002, $\eta^2 = 0.112$] and error rates [$F_{CxS}(9,63) = 6.52$, p = .002, $\eta^2 = 0.112$] and error rates [$F_{CxS}(9,63) = 6.70$, p < .001, $\eta^2 = 0.123$]. Priming effects in response times were present in all participants [p_C < .001; error rates: in all participants, p_C < .008], and

An overall 2 (C) x 2 (P) x 10 (S) ANOVA including the factor prime stimulus showed no difference in magnitude and time course of response time priming effects between control and Ponzo stimuli $[F_{CxP}(1,7) = 0.71, p = .482,$ η^2 = 0.004; F_{CxSxP}(9,63) = 1.86, p = .143, η^2 = 0.0171. Also, the higher magnitude of error rate priming effects in the shortest SOAs for Ponzo stimuli were only significant by trend $[F_{CxP}(1,7)]$ = 0.50, p = .504, η^2 = 0.004; $F_{CxSxP}(9,63)$ = 2.04, p = .050, η^2 = 0.023]. However, response times were about 10 ms faster $[F_P(1,7) =$ 21.69, p = .002, η^2 = 0.031] and error rates about 1 % lower $[F_P(1,7) = 5.16, p = .057, \eta^2 =$ 0.013] for control stimuli compared to Ponzo stimuli.

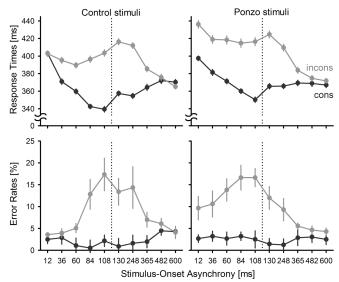


Figure 4. Results of the priming task for control stimuli (left panels) and Ponzo stimuli (right panels). Each panel displays mean response times (upper panels) and error rates (lower panels) in consistent (dark gray) and inconsistent trials (light gray) as a function of prime-target SOA. Dotted lines indicate the two sessions of the Experiment with either SOAs 12-108 ms or SOAs 130-600 ms. Error bars denote the standard error of the mean corrected for between-subjects variance (Cousineau, 2005; Loftus & Masson, 1994).

Thus, the single most evident difference between priming effects for control and Ponzo stimuli is that Ponzo stimuli did already yield a considerable effect with immediate succession of prime and target (i.e., at SOA = 12 ms). This difference was also significant in response times when performing an ANOVA within that condition and comparing both stimulus types via post-hoc contrasts $[F_{PxC}(1,7) = 9.69, p =$.017] (but was not significant in error rates, $F_{PxC}(1,7) = 3.54$, p = .102). However, we prefer to be cautious about this finding because priming effects are rarely reported (and much smaller) for immediate succession of prime and target - the prime has just not enough time to influence the motor response before arrival of the target. We speculate that the effect reported here might be following from an interference of the converging black lines in the primes with the subsequent targets as a result of their close temporal and spatial proximity. In inconsistent trials, the difference between the target bars might have been attenuated by the illusion, so that the relatively stronger primes might have had a larger influence on response times.

Response Primina task: time distributions. We varied prime-target SOA over a wide range and compared the respective priming effects induced by the illusion with that induced by control stimuli. However, the SOA is only one determinant of prime processing time. Another determinant is given by the spontaneous variation in a participant's response speed from trial to trial. If a participant is responding slower in a given trial, the visual system is provided with more time to process the visual information (e.g., to take context information into account). Therefore, we also analyzed priming effects for control and Ponzo stimuli as a function of response speed (Figure 5, for mean response times see Table 1). Notably, when the priming effects would increase in slower responses, this would indicate that the representation of the visual stimulus is not yet finished and stabilizing over time. In the case of the Ponzo stimuli, increasing effects in slower responses

would indicate that the illusion has not already taken full effect in the respectively faster responses.

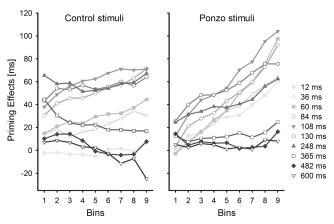


Figure 5. Response time distributions in the priming task for control stimuli (left panels) and Ponzo stimuli (right panels). Each panel displays mean priming effects as a function of response speed (bins 1 to 9), separately for the different levels of prime-target SOA (different symbols and shades of gray). Most notably, the priming effects for the control stimuli are constant or decreasing (exception at SOA = 84 ms) while those for the Ponzo stimuli are increasing at all SOAs ≤ 130 ms. Also, priming effects for the Ponzo stimuli are only larger than zero in the fastest responses for SOAs > 108 ms.

For control stimuli, variations in priming effects over the time course of responses were only significant at three levels of SOA, as tested by 2 (*C*) x 9 (*B*) ANOVAs. At SOA = 84 ms, priming effects increased in slower responses [$F_{CxB}(8,56) = 7.54$, p = .002, $\eta^2 = 0.115$; in 7 participants, $p_{CxB} < .003$] and at SOAs = 365 and 600 ms, effects decreased in slower responses [$F_{CxB}(8,56) = 3.58$, p = .043, $\eta^2 =$ 0.024; and $F_{CxB}(8,56) = 9.24$, p = .003, $\eta^2 =$ 0.038; in 5 and 6 participants, $p_{CxB} < .001$ and $p_{CxB} < .018$]. At all other SOAs, priming effects did not change over the time course of responses [$F_{CxB}(8,56) < 2.68$, p > .124, $\eta^2 <$

Table 1. Mean response times (with standard deviations) per bin. Response times are given in ms and rounded to full numbers for better legibility.

Bin	1	2	3	4	5	6	7	8	9
Stimuli									
Control	290 (39)	319 (31)	336 (31)	348 (31)	361 (31)	373 (34)	388 (37)	408 (42)	438 (59)
Ponzo	288 (39)	321 (31)	339 (32)	355 (34)	368 (36)	383 (39)	399 (42)	420 (50)	454 (63)

0.062]. The latter findings mirror the typical decay of response priming effects with SOAs > 130 ms (see also Jacob, Breitmeyer, & Treviño, 2013; Mattler, 2005): at some point, increasing processing time diminishes the influence of the prime (note that this decay is also visible for all but the last bin at SOA = 482ms). This finding is in accordance with accounts assuming that response priming effects (for "simple" visual stimuli) are predominantly driven by the first feedforward phase of information processing (e.g., Lamme & Roelfsema, 2000; Schmidt, Haberkamp, Veltkamp et al., 2011). This interpretation is somewhat inconsistent with the increase of priming effects in slower responses at SOA = 84 ms because this increase is typically not observed for SOAs < 100 ms (e.g., Schmidt, Weber, & Schmidt, 2014).

For Ponzo stimuli, the pattern of results is more clear-cut. In 2 (*C*) x 9 (*B*) ANOVAs, priming effects increased in slower responses at all SOAs \leq 130 ms [F_{CxB}(8,56) > 8.36, p < .002, η^2 > 0.068; at SOA = 12 ms and 36 ms in 7 participants, p_{CxB} < .001 and p_{CxB} < .001; at all other SOAs in all participants, p_{CxB} < .001] and at all SOAs \geq 248 ms, effects did not change over the time course of responses [F_{CxB}(8,56) < 2.89, p > .105, η^2 < 0.028]. This indicates that although an effect of the Ponzo illusion was already visible for short SOAs and reached a maximum around SOA = 108, it was only fully effective in the relatively slow responses of participants.

In sum, the effectiveness of the Ponzo illusion strongly depended on the time available. The more time the visual system had to process the Ponzo prime stimuli before the target signal entered the system (SOA; with a maximum around SOA = 108 ms) or before the motor response was executed (response speed), the stronger was the effect on the resulting motor response. While the effect of SOA seems to be very similar for control and Ponzo stimuli, that of response speed is dissociating both types of stimuli: while priming effects are strongly increasing in slower responses for Ponzo stimuli for SOAs \leq 130 ms, they only increase for control stimuli at SOA = 84 ms (or even decrease at long SOAs).

Discussion

Visual illusions offer the opportunity to investigate principal mechanisms of perception. However, these mechanisms are subject to changes over time: the perceptual representations of our environment develop typically over the first few hundred milliseconds after stimulus presentation. In the present study, we investigated the early time course of the Ponzo illusion - that might results from size constancy mechanisms (Gregory, 1966).

We tested whether Ponzo stimuli would induce priming effects in a primed flanker paradigm with short (12 ms) prime duration. We looked at the magnitude of these effects as a function of SOA and response speed to investigate the time course of the illusion and the temporal maximum in its influence on visuomotor processing. Finally, we tested the magnitude of the illusory effect in a traditional, perceptual task with the same stimuli and experimental surroundings to test for potential dissociations between temporally early and late processing phases in visual perception.

Our results show no dissociation between priming and perception. The strength of the illusion as measured in the perceptual task is similar to the difference between the bars in the control stimuli. Our results also show that control and Ponzo stimuli drive response priming effects in a typical manner: priming effects increase with SOA, and start to decay with SOAs > 130 ms (Jacob et al., 2013; Mattler, 2005). This decay is a consequence of the fact that response priming effects occur because the prime activates the motor response assigned to it (e.g., Klotz, Heumann, Ansorge, & Neumann, 2007; Vath & Schmidt, 2007) and this motor activation reaches a maximum at some point in time after the prime signal entered the visual system (Jacob et al., 2013). Thus, we demonstrate that the Ponzo illusion is active within the vision-for-action system and the induced priming effects are indistinguishable to those by control stimuli with bars of physically different size.

With respect to the influence of processing time, priming effects induced by the Ponzo illusion were increasing in slower compared to faster responses at all SOAs \leq 130 ms. This indicates that the representation

of the illusion at these SOAs was still developing (cf. van Zoest & Hunt, 2011). In general, this finding is in line with earlier findings that the magnitude of visual illusions changes over time (e.g., Piaget, 1961). More specifically, it shows that within the Ponzo stimuli the integration of task-relevant red bars task-irrelevant black lines and (context information) was not vet finished within the 130 ms between prime and target presentation. Given additional time, as in trials with slower response times, the integration was becoming more sophisticated and thus the illusion got stronger.

This strongly suggests that the integration of information across space that is necessary for the illusion to become effective, is not mediated by rapid feedforward mechanisms alone but is rather depending on more timeconsuming mechanisms. This might be modulatory feedback from higher to lower levels, or horizontal connections within levels of the visual hierarchy – given that they are even slower than feedback connections (Sugihara, Qiu, & von der Heydt, 2011).

Previous studies demonstrated an involvement of V1 in the representation of the illusory percept in context illusions (Fang, Boyaci, Kersten, & Murray, 2008; Murray, Boyaci, & Kersten, 2006). Based on our results, we argue that although the Ponzo illusion might be at some point represented within V1, it is very likely that either horizontal or feedback connections contribute to this representation and the resulting illusion. This is in line with previous arguments that these illusions are based on feedback from higher visual areas that are extracting threedimensional context of the background (Schwarzkopf et al., 2010; Song et al., 2011). At the same time, we observe an early effect of the Ponzo illusion that already develops from the second bin on (mean RT = 320 ms), showing that context is integrated online into the visuomotor response. At the same time, it is remarkable that the increasing effect of the Ponzo illusion is not reaching ceiling within the investigated range of response times priming effects are still stronger for the last bin compared to the second-to-last bin. Thus, although the Ponzo illusion can already manifest in motor responses based on presentation times of 12 ms, and for all SOAs

up to 248 ms, this manifestation is still subject to substantial sophistication when given more time. Note that this also implies that our study might underestimate maximum priming effects because we put time pressure on participants.

With respect to the ambiguous results of earlier studies concerning the time course of the Ponzo illusion (Luccio, 1969; Oyama & Morikawa, 1985; Revnolds, 1978), we can add evidence for the lower boundary of the temporal development of the illusory effect. In line with previous results, we found that there are quantitative changes in the illusory effect over the time course of processing. We findings corroborated these not by microgenetic methods (i.e., variation of presentation duration) but by varying SOA between primes and targets in a primed flanker paradigm, and, more importantly, by analyzing the resulting priming effects as a function of participants' response time (cf. Ratcliff, 1979; van Zoest & Hunt, 2011). Although it is difficult to compare our results directly to previous studies because of the difference in methods, the results can be analyzed on their own to identify the time course of the Ponzo illusion: the effect is building up over the time course of 300 ms (288 ms + 12 ms) to 702 ms (454 ms + 248 ms) (mean RT of the first bin plus the shortest SOA to mean RT of the last bin plus the longest SOA in which reliable priming effects importantly. are observed) and, this development is not finished even in the slowest responses of participants. Hence, our results may also explain the heterogeneous findings of previous studies. Clearly, а limitation of the presentation time does not imply that the required or available processing time is just as short: In principle, any short signal, once in the system, may be processed for an unlimited amount of time. Rather, presentation time limits the amount of temporal summation that can take place to form a reliable signal in the first place. Thus, previous studies ignored a fundamental aspect of temporal processing dynamics by ignoring the response times of participants (i.e., the actual time that the visual system invested in the processing of the illusion).

Moreover, the results of previous studies were certainly heterogeneous because the visual displays to induce the illusion were

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different. This was revealed by a pilot experiment, in which we tested a weaker variant of the Ponzo illusion with the two bars presented for 12 ms against two separate backgrounds (on the left and right side of fixation) with only two converging lines. This stimulus constellation produced onlv а relatively weak perceptual effect, presumably because the bars were more peripheral, not presented against a common background, and only against two (and not four) converging lines. As a result, we observed priming effects of Ponzo stimuli only at SOAs ≥ 84 ms. This is a clear call to caution when investigating the magnitude of visual illusions: even though the Ponzo illusion in both cases was pictorial and thus based on a very reduced number of features, the perceptual and visuomotor effects were dramatically different.

This might also be the reason why a previous study only reported effects of the Ponzo illusion on response times with at least 40 ms presentation time (Plewan et al., 2012). Here, we report definite evidence that the illusion already influences response times when it is presented for 12 ms only. This might be explained by the differences between measuring response times to the illusion versus the influence of the illusion on response times, or differences in the illusion display. Note, however, that Plewan et al. (2012) used a setting which specifically induced a two-dimensional perspective, thus inducing a more pronounced depth impression than our simple pictorial stimuli. This points to a remarkable fact: the magnitude of the priming effects for the Ponzo stimuli is comparable with the standard priming effects for the control stimuli. This is true although the Ponzo illusion is just based on a single, monocular depth cue, while under natural viewing conditions more depth cues are available (e.g., binocular disparity).

Plewan et al. (2012) state that their "data clearly show that combining context with different information neural representations such as retinal size requires visual information to persist for a minimum amount of time" (p. 373). Although this is certainly true, it seems that this minimum amount of time is not 40 ms but considerably shorter. Thereby, our results are also in line with previous findings showing that observers

can already retrieve some amount of distance information from visual displays presented as short as 9 ms (Gajewski et al., 2010). In our results, the perceived size of a stimulus presented for 12 ms is only neutral with respect to context-based size scaling when participants are responding fast. Only in these cases, there are no priming effects, indicating an early size coding that is presumably based on retinal size information.

What are the implications of our results with respect to the neurophysiology of the Ponzo illusion? Note that although our results might be in accordance with the notion that faster, more reflexive responses are refractory to visual illusions while slower, more voluntary responses are more susceptible to illusions (McCarley, Kramer, & DiGirolamo, 2003), recent evidence counteracts this notion (van Zoest & Hunt, 2011). In general, explaining contextual illusions in terms of the dissociation between a ventral pathway – that represents the relation between a visual target and its surrounding context - and a dorsal pathway that does not represent this relation and whose action output is unaffected by these illusions - has been challenged on empirical and theoretical grounds (Hamburger, Hansen, & Gegenfurtner, 2007; Schenk, Franz, & Bruno, 2011; for a review and discussion see Schenk & McIntosh, 2010). Besides other methodological factors, initial reports of a dissociation might have been due to a mismatch between the attributes guiding the responses in perception and action. Also, many studies have now demonstrated that visual illusions do affect actions.

Therefore, it is probably more instructive to explain our findings in terms of the different sub-pathways within the ventral pathway: a fast magnocellular pathway for rapid analysis of motion and low frequency spatial information and a slow parvocellular pathway that conveys high frequency information (e.g., Nowak & Bullier, 1997). In that context, it might be hypothesized that only the high frequency information of later representations, mediated by the slow parvocellular system, has the necessary resolution to identify, assign, and background relate target and context information.

Finally, our finding that the effect of the Ponzo illusion increases with increasing

response times, is related to the question of "relative" and "absolute metrics". Based on measurements of saccades, it is hypothesized that there is a passage from an "absolute" metric, in which the visual context is not yet fixed (feedforward processing), to a "relative" metric, which is typical of visual perception (recurrent processing; Bruno, 2001; de'Sperati et al. 2008: Hu and Goodale, 2000: Shi and de'Sperati, 2008). In this framework, our results would describe the development from an initial state without the inclusion of context information to a later perceptual state with the inclusion of context information. If the threshold of the motor responses is reached during the first state, no priming effects occur. When the threshold is reached during the second state, priming effects occur, reflecting integration of target and context the information in that perceptual state.

In this paper, we have used response priming methods to illustrate the time course

of the Ponzo illusion. Our results show a clear temporal development of the illusory percept and define a new, lower boundary for the occurrence of the illusion in response time effects.

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