The neural basis of form and form-motion integration from static and dynamic translational Glass patterns: a rTMS investigation

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Abstract

A long-held view of the visual system is that form and motion are independently analysed. However, there is physiological and psychophysical evidence of early interaction in the processing of form and motion. In this study, we used a combination of Glass patterns (GPs) and repetitive Transcranial Magnetic Stimulation (rTMS) to investigate in human observers the neural mechanisms underlying form-motion integration. GPs consist of randomly distributed dot pairs (dipoles) that induce the percept of an oriented stimulus. GPs can be either static or dynamic. Dynamic GPs have both a form component (i.e., orientation) and a non-directional motion component along the orientation axis. GPs were presented in two temporal intervals and observers were asked to discriminate the temporal interval containing the most coherent GP. rTMS was delivered over early visual area (V1/V2) and over area V5/MT shortly after the presentation of the GP in each interval. The results showed that rTMS applied over early visual areas affected the perception of static GPs, but the stimulation of area V5/MT did not affect observers' performance. On the other hand, rTMS was delivered over either V1/V2 or V5/MT strongly impaired the perception of dynamic GPs. These results suggest that early visual areas seem to be involved in the processing of the spatial structure of GPs, and interfering with the extraction of the global spatial structure also affects the extraction of the motion component, possibly interfering with early form-motion integration. However, visual area V5/MT is likely to be involved only in the processing of the motion component of dynamic GPs. These results suggest that motion and form cues may interact as early as V1/V2.

Keywords: static Glass patterns, dynamic Glass patterns, global form, motion-form integration, repetitive transcranial magnetic stimulation

Introduction

The visual system extracts complex spatial form by integrating many local orientation signals (Kourtzi et al., 2008; Krekelberg et al., 2003; Mannion et al., 2010, 2009; Murray et al., 2003; Or et al., 2010; Pavan et al., 2016; Ross et al., 2000). Stationary Glass patterns (GPs; Glass, 1969) represent a valid tool to investigate this integration process (Wilson and Wilkinson, 1998). Static GPs contain randomly distributed dot pairs (dipoles), whose orientations are determined by certain geometric transforms and convey the perception of either oriented or complex spatially distributed structures (Barlow and Olshausen, 2004; Clifford and Weston, 2005; Dakin, 1997; Dakin and Bex, 2001; Glass and Pérez, 1973; Glass and Switkes, 1976; Pavan et al., 2016; Wilson et al., 1997; Wilson and Wilkinson, 1998).

There is physiological evidence in macaque monkeys that simple and complex cells in visual areas V1 and V2 show orientation selectivity for static translational GPs presented in their classical receptive field (CRF; Smith et al., 2002, 2007). There is also human brain imaging evidence that supports the importance of the early visual areas in representing local orientation structure for the perception of complex spatial form (Mannion et al., 2010, 2009; Ohla et al., 2005; Ostwald et al., 2008). However, the absence of strong local contours in GPs causes the first stage of processing by orientation-selective cells to provide sparse and irregular orientation signals, and these signals need to be integrated by neurons tuned to global form (Smith et al., 2002, 2007). Several findings support the notion that sparse signal integration could take place as early as in V1/V2. Ostwald et al. (2008) found higher fMRI selectivity for translational GPs at lower stages of visual analysis (e.g., V1/V2), although pattern classification accuracy showed that translational GPs activate a wide range of extrastriate areas including V2, V3, V3A, VP/V3, hV4 and LOC (Krekelberg et al., 2005). Similarly, Mannion et al. (2010) showed an increased response to vertical dipoles and translational GPs in V1. Interestingly, they also reported sensitivity to curvature and global form across many early visual areas, including V1, V2, V3 and hV4. Taken together, these studies suggest that early visual areas not only process local orientation signals, but also contribute to their integration in global and complex structures.

In the present study, we used repetitive transcranial magnetic stimulation (rTMS) to investigate the causal role of early stages of visual processing in the perception of global form from static translational GPs. The rationale was that, if early visual areas play a role in the analysis of local orientation cues and their spatial summation, rTMS over these areas should impair observers' performance in detecting static translational GPs. We also investigated the neural basis of the perception of dynamic GPs. Dynamic GPs are created by sequential presentation of different stationary GPs, that convey the perception of (non-directional) motion (Krekelberg et al., 2005; Ross et al., 2000). An fMRI study by Krekelberg et al. (2005) reported that the human motion complex V5/MT does not distinguish between real motion and a non-directional motion percept induced by dynamic GPs; therefore, the representation of motion information in the human motion complex is invariant with respect to these two motion cues. Furthermore, there is psychophysical evidence that motion perception from dynamic GPs may rely on the extraction of motion streaks produced by the fast displacement of oriented dipoles (Burr and Ross, 2002; Geisler, 1999; Ross, 2004; Ross et al., 2000). Nankoo et al. (2015) showed that the coherence threshold for dynamic GPs is lower than that for static GPs, regardless of the structure used. The authors suggest that the lower coherence thresholds with dynamic GPs may depend not only on the extraction of motion streaks (i.e., strong orientation cues from non-directional motion) but also on the temporal summation of multiple form cues. This suggests that dynamic GPs are first processed as form stimuli (similar to their static counterparts) but are later processed as motion stimuli.

Previous psychophysical research has indicated that local orientation information in moving dynamic GPs (i.e., dynamic GPs with dipoles drifting in a specific direction), can affect their perceived motion direction (Krekelberg et al., 2003; Or et al., 2010), and that perceived global orientation is in turn influenced by motion direction, but to a lesser degree (Or et al., 2010). This suggests that motion and orientation information: a) interact asymmetrically; and b) interact at early stages of visual analysis (Dakin and Bex, 2001; Wilson and Wilkinson, 1998). Therefore, we also tested whether early visual areas are causally involved not only in the extraction of global form from static translational GPs, but also in motion-form integration when using dynamic GPs. If this is the case, rTMS over early visual areas

should also affect the observers' performance with dynamic GPs. rTMS was also delivered over V5/MT while viewing dynamic GPs. The rationale was that the motion component of dynamic GPs should be affected by interference with activity in area V5/MT (Krekelberg et al., 2005; Nankoo et al., 2015, 2012; Ross, 2004).

Method

Participants

Fifteen observers took part in this experiment. All participants had normal or corrected-to-normal visual acuity. Viewing was binocular. Each participant completed a questionnaire in order to assess for seizure, implanted metal objects, heart problems or any other psychiatric or neurological disease. Written informed consent was obtained from each participant prior to enrollment. Methods were carried out in accordance with the Declaration of Helsinki (1964). The present study was approved by the Ethics Committee of the University of Lincoln (protocol number: PSY1516138).

Apparatus

Stimuli were displayed on a 19-inch LCD Dell P190S monitor with a refresh rate of 60 Hz. Stimuli were generated with Matlab PsychToolbox (Brainard, 1997; Pelli, 1997). The screen resolution was 1280 x 1024 pixels. Each pixel subtended 1.7 arcmin. The minimum and maximum luminances of the screen were 0.17 and 191.7 cd/m^2 respectively, and the mean luminance was 41.5 cd/m^2. Observers sat in a dimly light room at a distance of 57 cm from the screen. The participant's head was stabilized by asking her/him to rest her/his chin on a chinrest.

Stimuli

The visual stimuli were static and dynamic translational GPs. Translational GPs were composed of 688 pairs of white (Weber Contrast: 3.62) dots (dipoles) (width of each dot 0.04 deg) randomly displayed within a circular annulus with an inner radius of 0.5 deg and outer radius of 4.5 deg. The pattern density was 10.95 dipoles/deg². Dipole length was 0.18 deg. We varied the coherence of the GPs; that is, a percentage of dipoles were vertically oriented (signal dipoles), whereas

the remaining dipoles were randomly oriented (noise dipoles), resulting in an orientation coherence ranging from 0% to 100%. Dynamic GPs were obtained by sequentially displaying a series of stationary GPs at a rate of 20 Hz (frame duration ~0.05 s). This temporal frequency was chosen on the basis of the findings of Nankoo et al. (2015), who showed low coherence thresholds for 20 Hz dynamic GPs with respect to static GPs. In dynamic GPs, for each new frame the spatial arrangement of the signal dipoles changed while their orientation remained fixed (i.e., vertical), whereas for noise dipoles both spatial location and orientation were randomly assigned. This produces a flickering texture in which apparent and non-directional motion is perceived along the axis parallel to signal dipoles' orientation (Krekelberg et al., 2005; Nankoo et al., 2012; Ross, 2004; Ross et al., 2000).

Procedure

The experiment consisted of two main sessions depending on the GP type used, i.e., static or dynamic. The presentation order of the two sessions was randomized across participants. The two sessions were administered in two different days. Every session consisted of four different phases:

Phase 1: Coherence threshold estimation

Each session began by measuring the participant's individual coherence threshold using a two-interval forced-choice task (2IFC). In one interval, there was a central static or dynamic translational GP (depending on the session) whose coherence was varied using a 1 up-3 down staircase (Levitt, 1971), whereas in the other interval a noise GP was presented. Observers had to judge which of the two intervals contained the most coherent GP (Figure 1). The temporal order of the intervals was randomized on a trial-by-trial basis. The coherence threshold corresponded to 79% accuracy in discriminating the interval containing the most coherent GP. The starting coherence of the translational GP was always 100%. The staircase was terminated after either 300 trials or 24 reversals. The coherence threshold was calculated by averaging the coherence estimated in the last 16

reversals. Each trial consisted of a fixation point presented for 1s, followed by two
0.3 s intervals separated by a blank interval of 0.2 s and an inter-trial interval of 2 s.
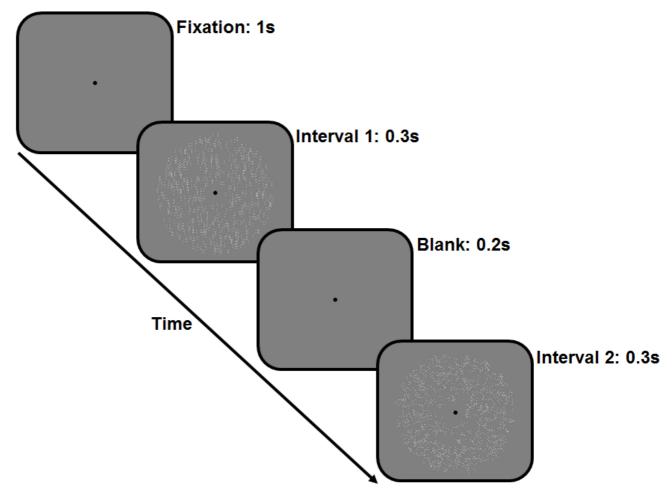

Figure 1. Schematic representation of the procedure. After an initial fixation point, a
vertical GP is shown in the first interval (100% coherence), whilst a noise GP is
displayed in the second interval (0% coherence).

Phase 2: rTMS stimulation and site localization

In order to localize the target cortical areas to stimulate and to set the TMS
intensity, the phosphene threshold was estimated individually for each participant.
rTMS stimulation was delivered through a MagPro X100 stimulator (Medtronic,
Denmark) with a figure-eight coil of 90 mm. Participants wore a swimming cap and
two stimulation sites were localized in all observers by using predetermined
coordinates: 3 cm dorsal to inion and 5 cm leftward from there for the localization of
V5/MT and 3 cm dorsal and 1 cm leftward from the inion for the localization of

V1/V2. Our decision to stimulate the left V5/MT is due to previous evidence which showed, using TMS, a lateralization of motion perception in the left hemisphere (Stewart et al., 1999; Antal et al., 2003).

Moreover, this localization technique has been used in previous studies (Campana et al., 2002, 2006, 2013; Laycock et al., 2007; Pascual-Leone et al., 1999; Pavan et al., 2011; Schenk et al., 2005; Silvanto et al., 2005; Stewart et al., 1999; Walsh et al., 1998) and provides a localization that is consistent with fMRI localizers (Thompson et al., 2009). These studies have shown that TMS applied over V5/MT is able to produce, in a proportion of participants, moving phosphenes. Thus, the induction of moving phosphenes is considered a reliable method which can prevent confusing V5/MT with other adjacent cortical areas. As a matter of the fact, five of our participants reported the perception of moving phosphenes during stimulation of V5/MT. When phosphenes were reported as non-moving, we considered the stimulation spot in which participants reported the most vivid phosphenes.

Additionally, we ran a control experiment in order to assess whether area V5/MT localisation based on the craniometric procedure overlays that based on neuronavigation (Brainsight, Rogue Research). Unlike all the other experiments, which were performed at the University of Lincoln, this experiment was conducted at the University of Padova where a neuronavigation system is available. We used the anatomical MRI scans of 15 new participants and localized area V5/MT using the Talairach coordinates of left V5/MT (on the normalized brain) found by Dumoulin and colleagues (2000): -47, -76, 2. Afterwards, on the same new sample of participants, we found the stimulation site by using the same craniometric procedure used in the main experiments; the skull position corresponding to 3 cm dorsal and 5 cm leftward from the inion. This time, however, by using neuronavigation we were able to estimate the center of the targeted area of the cortex holding the coil tangentially with respect to the skull surface. Finally, the distance between the sites found with the two procedures was measured. The results showed that the distance between the two sites was on average 7 mm (range: 2-10 mm) (Figure 2). Therefore, it is reasonable to assume that also on the craniometric measurements performed in the main experiment, this stimulation site was reasonably close to previously reported coordinates of V5/MT.

Moreover, in the main experiment the stimulation site of V5/MT was adjusted on the basis of the characteristics of phosphenes (e.g., moving, vivid, large), within 1 cm of radius from the point found with the craniometric procedure. Therefore, it is very likely that the stimulated area was V5/MT, rather than other more posterior areas such as V3B/KO or LOC.

Two cycles of 3 pulses (10 Hz) were delivered with an inter stimulation-interval of 0.2 s. This stimulation regime is the same as used in the main experiment. For the stimulation over V1/V2 and V5/MT, the coil was always held tangential to the skull with the handle pointing upwards. For stimulation over Cz the coil was held with the handle pointing backwards.

Observers verbally reported whether they saw any phosphenes. An adaptive procedure (i.e., REPT; Abrahamyan et al., 2011) was then used to estimate the rTMS intensity for which participants perceived phosphenes in 70% of the trials with eyes closed and blindfolded. Phosphene thresholds were estimated separately for V1/V2 and V5/MT and for static and dynamic sessions. All the participants perceived phosphenes. The mean rTMS intensity was 40.9% (SD: 4.6%) for V1/V2 and 41.9% (SD: 4.8%) for V5/MT. A paired t-test confirmed no statistically significant difference between the stimulation intensities over the two sites ($t_{14} = -1.308$, $p = 0.21$, *Cohen's d = 0.34*).
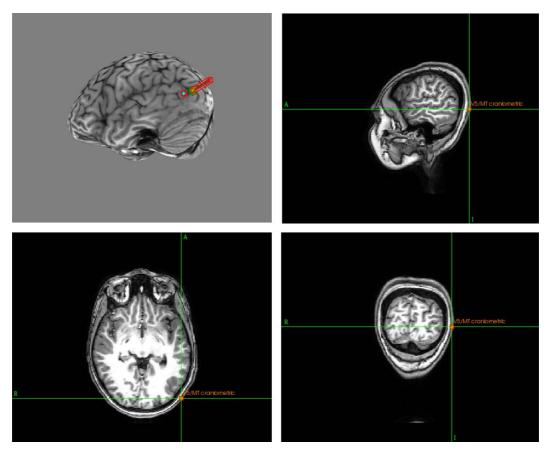
Figure 2. Representative participant of the neuronavigation control experiment with area V5/MT localized with both neuronavigation (based on the coordinates found by Dumoulin et al., 2000) and craniometric measurements. The top-left quadrant shows how localization of area V5/MT with neuronavigation is slightly more anterior (7.3 mm, cyan spot) with respect to the same area localized with craniometric measurements (green spot with normal vector to the skull surface depicted in red). In the other quadrants, the localization of area V5/MT based on craniometric measurements is shown on the participant's skull for sagittal (top-right), transverse (bottom-left) and coronal (bottom-right) views.

Phase 3: Assessing the level of accuracy at coherence threshold

After site localization and phosphene threshold estimation, observers performed the same 2IFC task described in phase 1, but the level of coherence was set at the individual coherence threshold determined in phase 1, and remained fixed across all trials. Observers performed 60 trials. If a participant failed to get an accuracy level in the range of 79% ± 2%, the number of coherently oriented dipoles

was manually adjusted in steps of five dipoles until their performance was within the aforementioned range. This procedure ensured that at the beginning of the rTMS sessions, all observers had approximately the same level of performance.

Phase 4: The main experiment

Observers performed 60 trials of the 2IFC task with the adjusted coherence level estimated in phase 3. In this phase of the Experiment, rTMS was applied over the target areas at the intensities determined in phase 2. rTMS pulses were delivered ~0.08 s after the onset of each stimulus interval and consisted of two cycles of three pulses at 10 Hz. This stimulation window was selected based on previous physiological and TMS studies on response latency in the primary visual cortex (Maunsell and Gibson, 1992; Nowak et al., 1995; Pascual-Leone and Walsh, 2001; Roebuck et al., 2014; Schmolesky et al., 1998; Silvanto et al., 2005). In order to control for nonspecific effects of the TMS stimulation, rTMS was also delivered over the vertex (Cz). In this rTMS condition, only phases 3 and 4 were performed, and the TMS intensity was set to the highest intensity between those used for V1/V2 and V5/MT stimulation. rTMS stimulation over V1/V2, V5/MT and Cz was performed within the same session. The stimulation order was randomized across participants and to prevent fatigue effects, the level of accuracy at coherence threshold for both static and dynamic GPs was assessed and adjusted before each rTMS condition (see phase 3 of the experiment).

Results

The mean coherence threshold was 25.6% (SD: 10.1%) for static GPs and 22.1% (SD: 9.6%) for dynamic GPs. A paired t-test confirmed a statistical significant difference between the coherence thresholds estimated for static and dynamic GPs ($t_{14} = 2.81$, $p = 0.014$, *Cohen's d = 0.72*).

Figure 3A shows the results of the experiment. A Shapiro-Wilk test found that all the independent variables were normally distributed ($p > 0.05$). A repeated measures ANOVA including as factors the GP type (static vs. dynamic) and stimulation site (V1/V2, V5/MT, Cz) reported a significant effect of GP type ($F_{1,14} = 4.98$, $p = 0.043$, *partial-η^2 = 0.26*), a significant effect of the stimulation site ($F_{2,28}$

= 16.08, $p = 0.0001$, *partial-η^2 = 0.54*), and a significant interaction between stimulus type and stimulation site (*F2,28 = 4.73*, $p = 0.017$, *partial-η^2 = 0.25*).

For static GPs, post-hoc comparisons using a false discovery rate (FDR) at 0.05 (Benjamini & Hochberg, 1995; Benjamini & Yekutieli, 2001), showed a significant difference between V1/V2 and V5/MT (*adjusted-p = 0.037*), and also between V1/V2 and Cz (*adjusted-p = 0.006*), while no significant difference was found between V5/MT and Cz (*adjusted-p = 0.99*). Additionally, we performed one-sample t-tests with FDR at 0.05 to assess whether following rTMS the observers' accuracy dropped below the 79% accuracy. The t-tests reported that only rTMS over V1/V2 significantly decreased the performance below 79% (*adjusted-p = 0.012*).

For dynamic GPs, post-hoc comparisons with FDR at 0.05, reported no statistically significant difference between V1/V2 and V5/MT (*adjusted-p > 0.05*), but a significant difference between V1/V2 and Cz (*adjusted-p = 0.0003*) and between V5/MT and Cz (*adjusted-p=0.003*). One-sample t-tests reported that rTMS over V1/V2 and V5/MT significantly decreased performance below 79% (*p = 0.0045* and *p = 0.003*, for V1/V2 and V5/MT respectively).

The analysis of the interaction between GP type and stimulation site also reported a significant difference between static and dynamic GPs only when rTMS was applied over V5/MT (*adjusted-p = 0.024*).

As evident in Figure 3B, this pattern of results was consistent for the majority of our participants. For static GPs, most of the observers showed higher accuracy when rTMS was delivered over V5/MT (i.e., data points fall mostly above the equal-performance diagonal), but for dynamic GPs, there is no consistent effect of the two stimulation sites (i.e., data points are distributed above and below the equal-performance diagonal).
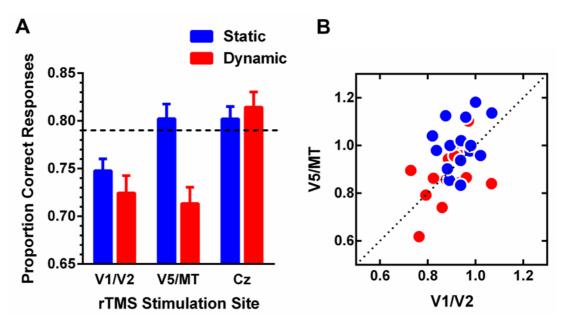
Figure 3. (A) Mean proportion of correct responses is reported as a function of the rTMS condition for static and dynamic GPs. The black dashed line represents the performance at threshold (79%). (B) Performance when rTMS was applied over V5/MT vs. V1/V2. Data points represent individual accuracies obtained for V5/MT and V1/V2 stimulations normalized by the Cz condition. The black dashed line represents the equal-performance line. Error bars ± SEM.

Discussion

In this study, we investigated the causal role of early visual areas (i.e., V1/V2) and the motion area V5/MT in the perception of global form from static translational GPs and motion-form integration using dynamic translational GPs. Observers had to discriminate which temporal interval contained the GP with the highest coherence. For static GPs, rTMS over early visual areas impaired observers' discrimination performance. These results suggest that early visual areas are involved in the extraction of global form, and rTMS may interfere with the analysis of local orientation signals and their spatial integration (Schmidtmann et al., 2015). On the other hand, rTMS applied over V5/MT had no effect in the discrimination of static GPs. These results are in agreement with previous human brain imaging studies that reported higher selectivity for static translational GPs at lower level of visual processing (Mannion et al., 2010, 2009; Ostwald et al.,

2008). The static GP results are also consistent with our previous findings that adaptation to static GPs induces a tilt-aftereffect similar to that produced using gratings, suggesting that adaptation to static oriented GPs is likely to tap low-level orientation selective mechanisms (Pavan et al., 2016). The results with static GPs also indicate that V5/MT is not involved in the extraction of global form, but it does seem to be involved in the extraction of the motion information from dynamic GPs: For dynamic GPs, rTMS affected the observers' performance when delivered over the cortical area V5/MT. This could reflect the disruption of the motion information present in dynamic GPs. Our results are consistent with the findings of Krekelberg et al. (2005) that the human motion complex processes non-directional motion from dynamic GPs. The response of area V5/MT to non-directional motion could be inherited from early visual areas in which neurons are orientation and direction selective. Albright (1984) found that macaque MT cells respond not only to moving stimuli but also to oriented stimuli, though to a lesser degree. In particular, Albright (1984) reported that 61% of the recorded cells exhibited an orientation preference nearly orthogonal to the preferred direction (as for V1 neurons), whereas 29% of the cells had an orientation selectivity almost parallel to the preferred direction. These results suggest that in MT area there are mechanisms selective to pattern-motion, and that orientation information could improve motion processing for high speeds (Geisler, 1999). Additionally, Kourtzi et al. (2002) found that a ventral sub-region of the human motion complex MT/MST is selective to both shape and motion. Taken together these findings suggest that area V5/MT is likely to be involved in motion-form integration. We argue that rTMS over visual area V5/MT may have interfered with the temporal integration mechanism that is the source of motion perception from dynamic GPs (Nankoo et al., 2015). Alternatively, the effect of rTMS over V5/MT for dynamic GPs could depend on the temporary disruption of the communication between V5/MT and early areas involved in fine shape analysis (e.g., V1/V2, V4, LOC; (Denys et al., 2004; Gallant et al., 2000; Kobatake and Tanaka, 1994; Krekelberg et al., 2005; Mannion et al., 2010, 2009). We suggest that the effect of rTMS over V5/MT for dynamic GPs could depend on the temporary disruption of the communication between V5/MT and early areas involved in fine shape analysis.

In fact, Koivisto et al. (2010) showed that a double-pulse TMS over V1/V2 at different inter-stimulus intervals (ISI), interfered with both feedforward and feedback information transmission between V1/V2 and V5/MT. The authors suggested that this could affect not only the processing of motion but also other stimulus attributes such as color and shape. In our study, stimulation over V5/MT may have also interfered with information transmission between V5/MT and early visual areas. Future studies applying single or double-pulse TMS at different time points may provide more insight into how form and motion information is transmitted in both a feedforward and feedback manner between V1/V2 and V5/MT.

rTMS also affected observers' performance with dynamic GPs when it was delivered over the early visual areas. In this case, rTMS may have interfered by increasing the excitability of less active neurons and therefore increased neural noise (Silvanto and Muggleton, 2008; Silvanto et al., 2008; Romei et al., 2016), or by suppressing the excitability of more active neurons processing form information to be forwarded to V5/MT (Perini et al., 2012), where the temporal integration of multiple static structures may occur.

Alternatively, rTMS may interfere with motion-form integration at early levels of visual processing: There is recent brain imaging evidence that early visual areas process both motion and form cues and neurons integrate these signals. Apthorp et al. (2013), used fMRI to measure brain activity while human observers viewed either fast moving dots (eliciting motion streaks; Geisler, 2000), slow moving dots, or static oriented stimuli. The authors found that local spatial patterns of brain activity in early visual cortex reliably distinguished between static orientations. Additionally, they found that a multivariate pattern classifier trained on the brain activity evoked by static oriented stimuli could discriminate the direction of fast moving dots producing motion streaks, but could not discriminate the direction of slow moving dots. This suggests the presence of early visual mechanisms that encode static oriented information (i.e., oriented streaks) when viewing fast moving objects. These findings show that motion streaks are likely to be extracted in early stages of visual analysis, implying that motion and form are processed and combined at early stages of visual analysis

and that static oriented information can aid motion direction discrimination (Burr, 1980; Burr and Ross, 2002; Geisler, 1999; Ross, 2004; Ross et al., 2000). In our study, rTMS over V1/V2 when using dynamic GPs may also have interfered with form-motion integration, preventing the extraction of motion streaks, thought to be involved in the perception of dynamic GPs (Ross, 2004). However, our TMS findings cannot disentangle these two alternatives, and further brain imaging research is necessary to investigate the interplay between form and motion signals in striate and extrastriate areas. Nonetheless, it seems that global form and motion information are extracted and combined at early stages of visual analysis (Mather et al., 2013).

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