



# Article An ART Tour de Force on Mental Imagery: Vividness, Individual Bias Differences, and Complementary Visual Processing Streams

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Abstract: Grossberg's adaptive resonance theory (ART) provides a framework for understanding possible interactions between mental imagery and visual perception. Our purpose was to integrate, within ART, the phenomenological notion of mental image vividness and thus investigate the possible biasing effects of individual differences on visual processing. Using a Vernier acuity task, we tested whether indirect estimation of relative V1 size (small, medium, large) and self-reported vividness, in three subgroups of 53 observers, could predict significant effects of priming, interference, or more extreme Perky effects (negative and positive), which could be induced by imagery, impacting acuity performance. The results showed that small V1 was correlated with priming and/or negative Perky effects independently of vividness; medium V1 was related to interference at low vividness but priming at high vividness; and large V1 was related to positive Perky effects at high vividness but negative Perky effects at low vividness. Our interpretation of ART and related modeling based on ARTSCAN contributes to expanding Grossberg's comprehensive understanding of how and why individually experienced vividness may drive the differential use of the dorsal and ventral complementary visual processing pathways, resulting in the observed effects of imagery on concurrent perception.

**Keywords:** adaptive resonance theory; imagery; perception; vividness; visual cortex; visual priming; perky effect

# 1. Introduction: ART and Vividness of Visual Mental Imagery

Grossberg's adaptive resonance theory (ART) provides a robust framework for understanding how imagery–perception interactions occur in complementary dorsal and ventral cortical visual processing. The objective of this paper was to integrate within ART a phenomenological component based on the classic psychological notion of mental image vividness [1] to supplement the "how" explanation with a "why" explanation describing processing biases which are associated with individual anatomical differences.

The vividness of mental imagery has been studied for more than a century in psychology and is traditionally defined as a quasi-perceptual (predominantly *visual*) *phenomenological* experience [2–5]. In his comprehensive theory combining phenomenological and behavioral perspectives, Marks [3,6] posits vividness as a dynamic process guided by intentional, conscious, and voluntary executive and regulatory mechanisms embedded in generating and using visual mental imagery. This dynamic, processual view of vividness aligns with Grossberg's view of an "emerging theory of imagery" in the neuroscience domain as "…part of a larger neural theory of visual seeing and thinking" ([7], p. 195).

The rapid advancement of the neuroscience of vision (often inspired by Grossberg himself) has led to many new findings on mental images and has led to increased interest in vividness. For most people, generating visual mental images depends on the same neural and functional mechanisms involved in seeing. Imagery and perception involve not only similar mechanisms, but also similar synchronizations across brain areas [8].



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**Copyright:** © 2024 by the authors. Licensee MDPI, Basel, Switzerland. This article is an open access article distributed under the terms and conditions of the Creative Commons Attribution (CC BY) license (https:// creativecommons.org/licenses/by/ 4.0/). Moreover, physical representations and imagined scenarios both influence the detection of target stimuli. Thus, studies have emphasized that early visual areas impact both the top-down generation of images during mental imagery and the vividness of images retrieved from memory [9]. While some findings suggest similar underlying mechanisms for visual imagery and visual perception, other findings suggest an overlap, and some research suggests equivalent mechanisms [9]. These overlaps in the top-down connectivity of neural mechanisms in perception and imagery—which are a necessary ingredient of ART—suggest a consistent relationship between mental imagery and the functional impact of conscious perception [10]. Using imagery, ambiguous stimuli can be formed into more precise and stable visual perceptions. As a paradigmatic example, vividness can induce bias, which determines the dominant perception of one of two binocularly different color patches [11]. Grossberg's approach, however, is an important advancement. Not only does it describe the contextually dependent differential variants of top-down connectivity and the influence of bottom-up processing on imagery, but also, it seamlessly integrates phenomenological components as a causally relevant and non-epiphenomenal aspect of consciousness within the same unitary model. Thus, Grossberg's idea of resonance in ART can be extended to create an implementable neural model of vividness of mental imagery. Following the ART rationale, vividness may depend on the complex functional links among the processes of consciousness, learning, expectation, attention, resonance, and synchrony (CLEARS) [12].

According to Grossberg [12], resonance occurs among different brain areas. The brain areas associated with perception and imagination communicate dynamically, resulting in the construction of mental images. In this process, resonance reflects the synchronization of neural activity between brain areas (particularly the ventral and dorsal streams), and increased resonance between such areas leads to stronger connections and the integration of more information [12]. Thus, the strength of resonance between areas involved in imagery and perception may be related to the vividness of the mental images. The topdown and bottom-up feedback recurrent connections utilizing the dorsal and ventral streams allow for the precision, refinement, and enhancement of the vividness of the image. Specifically, the high-level mechanisms that control the selective detection of change need a modulating factor that makes attention a phenomenologically vivid reality (as per William James's famous dictum: "...the taking possession by the mind, in clear and vivid form..." https://psychclassics.yorku.ca/James/Principles/prin11.htm, accessed on 1 September 2023). Consistent with the assumptions of ART [12,13], we argue that the topdown voluntary processing related to the vividness of imagery is important for distributing attention and contributes to the categorization, recognition, and prediction of objects. Externally and internally directed attention determines our ability to learn and adjust neural patterns [14]. While externally directed attention determines the objects, features, and spatial locations of what we see in our visual field, the mechanisms of internally directed attention are less known, and their connections to imagery and vividness have not yet been clarified [14]. An exception is a study by Gjorgieva et al. [15], who reported a clear relationship between attention and image vividness, showing that the latency of parietal ERP signatures of internally directed attention was inversely related to image vividness, replicating an earlier behavioral finding of D'Angiulli and Reeves [16], namely, that vividness was associated with faster processing.

#### 1.1. Review of Related Imagery Research

In most individuals, visual mental images do not impact the accuracy of visual perception (i.e., how well an individual resolves external visual stimuli). In other individuals, however, concurrent mental images do impact perception by either augmenting or decreasing baseline visual performance. These facilitation and interference phenomena have been widely recognized and studied in the field of perception, where they are traditionally known as priming and interference, or negative and positive Perky effects, respectively [17]. However, negative and positive Perky effects are generally considered absolute changes in accuracy of approximately  $\pm 5\%$  relative to the acuity baseline, while the corresponding priming and interference effects are relative within-subjects changes that could be empirically smaller but significant numerical deltas. Very recent findings from cognitive neuroscience studies (generally involving functional magnetic resonance imaging (fMRI)) have confirmed and extended previous findings (generally involving electroencephalography (EEG) or event-related potential (ERP) (see review in [18])) on the neural correlates of the VVIQ and trial-by-trial vividness ratings based on instructions that emphasize sensory strength (see reviews in [1,19]). Furthermore, other behavioral evidence has shown that vividness can prime stimulus detection [18], and several reports have shown that image vividness impacts visual sensitivity (see [17–21]).

Recent research has shown that the size of V1, the precision of visual acuity, and the vividness of mental imagery are related. The average or baseline accuracy of visual processing or visual precision can be assessed by tasks measuring accuracy in resolving detailed information in perceptual visual images, such as the Vernier acuity task, a standardized and validated paradigm [17]. In one version of this task, participants report the side of the visual hemifield (left or right) in which offset parallel line segments appear, either monoor binocularly. By instructing participants to generate visual mental images while presenting Venier acuity targets, it is possible to empirically show whether imagery increases or decreases task performance (i.e., improves or hinders visual acuity, respectively) [16,17]. Importantly, Venier acuity is correlated with cortical magnification and the size of receptive fields in V1, making it a reliable behavioral proxy indicator of V1 size [22,23].

Bergmann et al. [21] showed that priming and interference depend on an individual's accuracy (i.e., visual precision); however, importantly, individual differences in visual precision differ from individual differences in sensory strength and can be associated with differences in the size of V1. Namely, when asked to create a concurrent visual mental image, individuals with a typical (medium) V1 size had average visual precision and showed no change in visual precision relative to baseline. However, individuals with larger V1 areas demonstrated above-average visual precision and with concurrent imagery, showed priming effects. In contrast, individuals with relatively smaller V1 regions demonstrated average visual precision and with concurrent imagery, showed "sensory" interference.

Although Bergmann et al.'s [21] study was successful in elucidating the neural early visual correlates of individual differences associated with mental imagery, they only partially clarified the neural substrate of vividness. Despite the finding that vividness was related to the prefrontal cortex (PFC) volume, they did not clarify how individual differences in vividness judgments reflect individual differences in V1 or how individual characteristics in early visual processing are driven by changes in PFC activity. Kosslyn and colleagues [24] suggested that during visual processing, the magnocellular pathway in the dorsal stream is recruited for spatial imagery tasks (locating objects), while the parvocellular pathway in the ventral stream is mainly recruited for object imagery tasks (identifying objects) [13]. The dorsal stream is recruited more in individuals with stronger sensory interference, while the ventral stream is recruited by individuals with stronger visual precision but weaker sensory interference (as per Bergman et al.) [21]. Based on this evidence, individual differences in the size of V1 might be correlated with recruitment of the dorsal and ventral pathways. D'Angiulli et al. [25] performed ERP and EEG studies, demonstrating hemispheric asymmetry during mental image generation, which reflects the differential distribution of activity in the dorsal and ventral pathways; magnocellular neurons associated with spatial precision ([24]) are mainly active in the right dorsal electrode sites, whereas parvocellular neurons associated with object shape ([24]) are mainly active in the left ventral electrode sites. Importantly, ERP activity and polarity in prefrontal regions were inversely correlated with those in the occipital regions. The latter finding cannot be explained according to EEG operation, as the inversely correlated activity was selectively identified only between those electrode sites and not within the other sites. The same electrode selectivity was also found for anticorrelated synchronization and desynchronization of EEG power involving alpha, beta, and theta band frequencies.

Kosslyn's work has been fundamental to the imagery research field. Nevertheless, it has also biased the field so that researchers now widely assume an underlying natural taxonomy of different mental representations matched with various neural systems or mechanisms. On this basis, individual differences are derived from the preferential mechanism or modules used and the characteristics of particular tasks that require images, which determines the alternate predominance of either the dorsal or ventral streams (for example, see [26]). In contrast, according to Grossberg [27], both the ventral and the dorsal streams always maintain complementary *parallel* cortical processes [27]. The dorsal stream includes the spatial and motor processes that control adaptation based on changing bodily parameters. Moreover, the dorsal stream involves spatial representations, whereas the ventral stream is specific and does not consider object views, positions, or sizes. Therefore, as Grossberg [27] described, the two streams operate in parallel to perform actions according to the specific object and scene, incorporating the processes of the ventral and dorsal streams accordingly. This corresponds to the key principle of complementary computation, according to which complementary cortical streams coordinate their activity reciprocally and dynamically to synergistically overcome their "weaknesses", namely, their limitations due to their modular rigidity and biomolecular boundedness in processing independent isolated aspects. He described the two coordination dynamics as what-to-where and where-to*what* excitatory and inhibitory parallel interactive learning pathways. However, we suggest that image vividness may bias the weight of processing by recruiting one stream more than the other, acting as another complementary or competing process to the attention given to a visual object. That is, visual "images" are not the same as consciousness; they have a phenomenological gradient corresponding to the strength of resonance, which might reflect higher-level complementary dynamic processing from the top-down inputs to V1. Therefore, if the two streams are imbalanced, the view, position, or size of an object may be incorrect or unable to adapt to changing parameters; thus, the spatial context of the object may be unknown. The top-down interactions of these streams include object and spatial attentional processes that could influence whether imagery hinders or facilitates visual processes. Furthermore, the extent to which the dorsal and ventral streams influence the direction of internal attention may determine whether visual processes are hindered or facilitated by mental images [27].

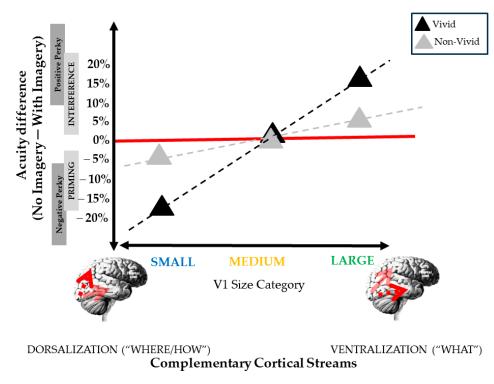
To determine the nature of the vivid-is-fast relation, D'Angiulli and Reeves [28] modeled latencies of visual mental image generation under several visual angle (foveal and parafoveal) conditions to probe magnocellular (mainly dorsal) versus parvocellular (mainly ventral) pathways and measured concurrent trial-by-trial vividness ratings after instructing the observers to report sensory strength rather than details of the contents (see [5]). Based on the best available functional mapping of streams of information processing during image-related tasks [29], these data suggest that vividness ratings increase when they reflect fast judgments, presumably corresponding to the involvement of frontal areas based on input from ventral streams (ventralization), whereas ratings decline when the same observers make slower judgments (still presumably controlled by frontal areas) based on inputs from dorsal visual pathway streams (dorsalization) [28].

#### 1.2. The Present Study: Hypotheses and Predictions

If, as the reviewed evidence suggests, individual differences in visual processing can bias how images are accessed and consciously self-reported, then more interference or priming could reflect disequilibrium between dorsal and ventral processes, which is linked with individual anatomical differences and levels of vividness. This is the central tenet we aim to investigate in the present study *from within* Grossberg's ART framework.

Following D'Angiulli and Reeves [27] and Kosslyn et al. [24], we hypothesize that a large V1 should correlate with top-down ventralization (top-down ventral dominance), whereas a small V1 should correlate with top-down dorsalization (top-down dorsal dominance). To test these hypotheses, we devised an experiment in which participants were asked to generate a visual mental image of their own choice (under strict image guidelines)

and project those images onto a screen where the observers had to simultaneously detect a Vernier acuity target (i.e., an offset line). This experimental design allowed us to investigate the degree to which imagery influences the perception of fine acuity stimuli. The predicted outcome scenarios derived from the hypotheses are presented in Figure 1.



**Figure 1.** Schematic representation of the predicted outcomes for the interaction between visual mental imagery and target perception as a function of V1 size and complementary processing streams. Red line indicates no effect of imagery over acuity referencing baseline equilibrium between dorsal and ventral streams.

We expected that large, ventrally dominant V1 regions would direct attention internally within the ventral/what pathway (corresponding to Grossberg's "object shroud" [13]) in the case of high vividness, which should interfere with attentional resources directed externally to the position of the concurrently presented visual target (Grossberg's "spatial shroud" [13]), thereby disrupting the what-to-where stream. In this scenario, the whatto-where pathway should compete with where-to-what processing, resulting in reduced detection of the target spatial position (i.e., positive Perky effects). However, in the case of low vividness, the overlap in parvocellular processing between imagery and concurrent acuity would be minimal, and this competition among the pathways should be significantly reduced. In contrast, individuals with small, dorsally dominant V1 regions should perform mostly magnocellular processing and show minimal overlap between parvocellular processing and concurrent acuity, with this overlap further reduced in the case of low vividness. In this scenario, the what-to-where pathway should compete with where-towhat processing. Consequently, priming should occur at both vividness levels for small V1 processing, with more extreme priming (i.e., negative Perky effects) observed for low vividness. Finally, according to Bergman et al. [21], we predict that medium V1 regions should engage parvo- and magnocellular pathways approximately equally, balancing competition and cooperation among the two streams. Accordingly, in this case, vividness should bias attention by enhancing or reducing attention toward the target primarily through the what-to-where pathway; thus, we expect moderate priming effects for high vividness and moderate interference effects for low vividness, the opposite to what should occur for the case of large V1.

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## 2. Materials and Methods

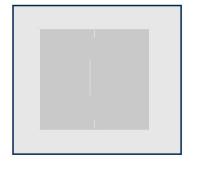
## 2.1. Participants

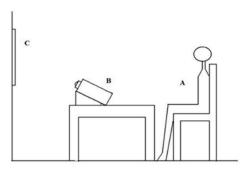
Initially, 60 first-year undergraduate psychology students aged 18 to 25 years (M = 22, SD = 1.75) were recruited to participate through Carleton University's Student Organization of North America (SONA) subject recruitment system. Inclusion in the study was conditional on signing a written informed consent form. The Institutional Behavioural Research Ethics Board of Carleton University approved this study (protocol code 111569 27 November 2019), which was conducted in conformity with the Declaration of Helsinki and Canada's Tri-Council Policy Statement.

Among the participants, 53% identified as male and 47% identified as female. In the preliminary phase of the study, the participants underwent personality and imagery screening using the VVIQ and the Big Five Inventory [30]. The VVIQ was the first questionnaire the participants completed. Participants practiced visualizing while completing this questionnaire. Following the standard procedure, the participants were presented with the 16 VVIQ descriptions and asked to rate the mental images that came to their minds on a scale of 1 (perfectly clear) to 7 (no image). Only data from participants who scored within the typical range (within 2 SD of the grand mean) in both questionnaires were included in the present study. Two candidates obtained the minimum possible score on the VVIQ, while five candidates scored below the norm on one of the items in the Big Five Inventory; therefore, their data were not included in the analysis. Finally, after screening, 53 participants were included; twenty-nine participants received a psychology course credit of 1.5%, whereas twenty-four participants were volunteers who did not receive any compensation. Preliminary inspection and analysis of the data did not reveal statistically significant differences between these two groups (multivariate test of the variance difference between the scores from the two samples in all eight no-imagery and imagery conditions yielded the following summary statistics: Hotelling's trace = 0.28 (df: 8, 51);  $p \sim 0.20$ ).

## 2.2. Apparatus

The stimuli and background were projected onto a white screen mounted on a wall by a Sony Duocom LCD Data Projector (XGA VPL-CX1, Sony Electronics Inc., Park Ridge, NJ, USA). Projections were controlled by the experimenter using a keyboard connected to an LG Prosys computer, which also ran the computer program displayed by the projector and recorded the data for the visual acuity task. The stimuli were generated, displayed, and controlled using the Visual Basic program. The experimental setup is graphically represented in the right panel of Figure 2.





**Figure 2.** Schematic of the experimental setup. **Left** Panel: Actual screen appearance of the offset lines used for the acuity test. The particular offset in the shown trial is on the left visual hemifield (hence the correct response was "left"); note that the lines are not drawn to scale. **Right** panel: Participants (represented in (**A**)) were seated directly in front of the projected stimuli (represented in (**B**)) Stimuli were projected using a Sony Duocom LCD data projector (**B**). The stimuli were projected on a white screen mounted on a wall perpendicular to the participant's field of vision (represented in (**C**)).

## 2.3. Stimuli and Procedure

Participants were tested individually and seated in front of a table, upon which the projector rested (see Figure 2, right panel). The experimenter sat on the left of the table. Participants were asked whether they knew what mental imagery was and if they could generate one as an example. In the initial familiarization and subsequent practice phases, participants were encouraged to verbalize and describe their images.

Participants started the experimental session by completing the VVIQ and the TSDVI. The experimenter verbally explained the task instructions (adapted from the Appendix of ([28]; pp. 544–546); the modification concerned the response modality, which was changed in the present procedure). Vividness was defined as "the extent to which the imagined object is lifelike or resembles real seeing" ([28]; p. 545). Examples of vivid imagery (e.g., your mother's face) and nonvivid imagery (e.g., your kindergarten teacher's face) were provided, and participants were asked to provide some examples. The terms dynamic image ("something moving") and static image ("not moving" and "still") were described, and examples were provided (e.g., a Canadian flag blowing in the wind, a face not talking or moving at all). The latter was adapted from a previous protocol ([30]; Experiment 2). Participants were asked to generate other examples, verbalize and describe their experiences, and share their self-rating of vividness. To self-rate the vividness of their images, participants were asked to use the same 7-point Likert scale as the one used for the VVIQ items (i.e., from 1 = perfectly clear to 7 = no image). Following completion, both questionnaires were removed, and the participants started the visual acuity task trials.

The next phase of the experimental procedure for the actual acuity task session was adapted from the standard protocol for ERP and EEG data collection used by D'Angiulli et al. [25] (in the present experiment, only behavioral data were collected). Although the main focus of the present study was to compare vivid and nonvivid static visual mental images, two classic issues in the formation of imagery are the level of voluntary control and the incorporation of dynamic images. Both aspects may involve moving images. Previous research has shown that static imagery is significantly more vivid than dynamic imagery of the same content [31,32] and might be more difficult to voluntarily control. This might be due to the involvement of key areas of the dorsal stream, such as the MT [32]. Thus, we instructed the participants to generate vivid and nonvivid moving images, as a secondary objective was to explore whether asking participants to generate moving images might bias dorsal recruitment. Therefore, the instructions were changed according to the block of trials so that each participant was asked to produce images under previously validated instructions [28,32], yielding types of four mental image: static vivid (SV), dynamic vivid (DV), static nonvivid (SNV), or dynamic nonvivid (DNV). A fifth condition involved performing the acuity task without generating any mental image (no image, NI). In the static and dynamic conditions, participants were instructed to start the experiment by generating a small set of 2–3 images with consistent vividness self-ratings between 2 and 3 to define the vivid images, while another set of images with vividness ratings between 6 and 7 were used to define nonvivid images. To assess V1 size through neuropsychological methods, the NI condition and its associated visual acuity score served as indirect measures of an individual's V1 size, given that visual acuity is associated with the size of V1 [22,23]. One type of mental image or NI was used in each block of trials, and the order of the image types was randomly determined before the experiment using a free, online random number generator (http://www.random.org/ (accessed on 17 January 2024). The NI and the four mental image types created 5 experimental conditions. There were 5 practice blocks (1 for each mental image type and 1 for the NI condition) of 5 trials each. The experimental trials consisted of 16 blocks of 10 trials each, with 8 blocks of mental images and 8 blocks of NI. (All executable programs for the experiment can be publicly viewed and downloaded from doi:10.5281/zenodo.10076451).

For the Vernier acuity task, the room was dimly lit at lighting settings approximating D'Angiulli et al. [25]. Participants were told that at any point, they could stop the experiment and take a break or have the lights turned on. A white screen measuring 1 ft  $\times$  1 ft

was mounted on the wall, 4 ft. away from participants. The surface was painted on a black background, and a pair of thin, vertical white lines 5 mm long was placed at the center, with the lines stacked and separated by approximately 2.3 in (5.84 cm). A third thin, white vertical line (approx. 5 cm long) between, and slightly offset (approx. 2 mm left or right), from the two shorter lines was displayed for 68 ms by the experimenter for each trial on cue. This stimulus line was the target (see Figure 2, left panel). The complete line displays a subtended 2.62° visual angle. The line was displayed on a black background using a standard CRT monitor ( $11 \times 19.5$  cm). The contrast and brightness were set to a minimum, and the color was set to grayscale. The task corresponded to photopic conditions, with an approximate luminance of 50 cd/m<sup>2</sup> and a Weber contrast of 21:1 (as in [26]).

Cues came from the participant, either by verbally saying "ok" or clicking a retractable pen to indicate that a mental image was being generated. During each image trial, participants were asked to look between the two short lines and to imagine a specific image (as indicated by the experimenter). When the generated mental image was sufficiently stable, participants were asked to cue the experimenter, who then clicked the mouse; the experimenter's mouse click caused the long line (target) to flash for a duration of 67 ms, either to the left or right of the two short lines (presentation side was random). Participants, while holding onto their image, viewed the line and indicated which side they thought the line appeared on by saying "left" or "right" (see left panel of Figure 2). If uncertain, participants were instructed to give their best guess. *No image* (NI) trials proceeded similarly, but participants were instructed not to produce mental images during the acuity task. Participants took as much time as they needed between trials to ensure that their images were strong and reliable for each trial. If the patient was distracted or if an image was lost while completing a trial, the entire block was discarded, and the patient began a new trail.

Most participants had no difficulty understanding the different mental image types, as indicated by their own examples. Only three participants required extra practice. These participants were either given 5 extra practice trials for each image type or repeated the incomplete block. The experiment lasted approximately 1.5 h. Participants were debriefed following the visual detection task.

#### 2.4. Analytical Approach

Participants' scores were recorded as a percentage of the total correct responses (accurately answering if the stimulus line was on the left or right side) in the visual detection task over each block of 10 trials. As the blocks for each mental image type were randomly selected to include two imagery blocks and two no-imagery blocks, the results yielded scores  $\geq$ 20 for NI and >20 for each mental image type. These scores were then transformed into percentages of correct responses. The computer data acquisition program automatically rounded percent values to the closest integer real number without decimal places. The performance scores were calculated as NI % correct—image % correct. In other words, the image trial correct scores were subtracted from the NI trial correct scores to obtain a percentage, which was either negative or positive. Positive scores indicated interference, and negative scores indicated priming. Based on criteria similar to those used in the current literature [16], interference corresponding to a score difference of  $\geq$ 5% was defined as a *positive Perky* effect, while priming corresponding to a score difference of  $\leq$ -5% was defined as a *negative Perky* effect.

In the first analysis, we described the overall distribution of all effects without parametric (i.e., normality) assumptions. Performance scores were calculated for each participant for each mental image type (including dynamic images). No result (0% or "null" effects), interference (including positive Perky effects), and priming (including negative Perky effects) cases were subdivided into 3 categories, and each effect score (NI imagery) for each mental image type was subjected to the Kruskal–Wallis test (nonparametric repeated-measures ANOVA). Subsequently, for each mental image type, interference and priming data were compared using two independent sample tests (Mann–Whitney test) to explore possible post hoc differences following the initial Kruskal–Wallis test. In the subsequent analysis, following confirmatory parametric diagnostics showing tolerable deviation from normality, we focused primarily on static imagery, and we regressed the effect of imagery on concurrent acuity accuracy (as % difference scores) against baseline acuity performance. As a secondary analysis for completeness, we performed the same analysis for the dynamic imagery to provide a comparison for reference. We converted the r coefficients to Zr scores as a polynomial contrast to test for trends. Multiple t tests with Simes–Bonferroni adjustment were applied to determine significant differences between mental image types, including polynomial linear pattern tests. Simes–Bonferroni adjustment yielded a threshold of p < 0.03, corresponding to a critical t value of 2.021 (df = 51).

Finally, to investigate the relationship between interference, priming and Perky effects, and the size of V1, we scaled all the measured percentage difference scores using the average NI collapsed on all blocks subtracted from each condition and tested between-subject effects using a three-way repeated measures hierarchical mixed model ANOVA with the following factors: V1 size (3 levels: small, medium, large)  $\times$  vividness (vivid vs. nonvivid)  $\times$  image type (static vs. dynamic). We included subjects as a covariate to control for individual subject variance. The categories of relative V1 size were extracted from the empirically observed distribution of baseline visual acuity performance scores, under the assumption derived from previously reviewed literature that visual sensitivity is a proxy for V1 size. There exists no accepted absolute partition of V1 size based on this indirect measurement method; therefore, we divided the observed interval of scores arbitrarily in three ordered bins of same data density. Based on the intervals of baseline acuity performance in the NI condition, V1 was categorized into three groups as follows: small, corresponding to a baseline performance interval between 20% and 45%; medium, corresponding to a baseline performance interval between 46% and 55%; and large, corresponding to a baseline performance interval between 56% and 90%. These defined the three relative size group categories used to empirically test the predictions represented in Figure 1.

#### 3. Results

### 3.1. Interference and Priming Distributions

For all mental image types, effect scores by group were found to be significant (for SV:  $\chi^2(2) = 35.02$ , d = 2.79; for SNV:  $\chi^2(2) = 36.41$ , d = 2.96; for DV:  $\chi^2(2) = 38.16$ , d = 3.21; for DNV:  $\chi^2(2) = 39.10$ , d = 3.34; for all tests, N = 53 and *p* < 0.0001). The results showed that for all mental image types except DV, the proportion of participants who showed priming and/or negative Perky effects was greater than the proportion of participants who showed interference and/or positive Perky effects, and the distribution of the effect scores significantly differed, showing that the differences in the types of effects observed were not due to chance. The number of participants experiencing each effect, the proportion, and the mean rank for each image type are shown in Table 1.

**Table 1.** Proportions (and n) of participants experiencing interference/positive Perky effects, priming/negative Perky effects, or null effects for each type of imagery.

		Image	Types	
	Static		Dynamic	
-	Vivid	Nonvivid	Vivid	Nonvivid
Effect type				
Interference	32.1 (17)	43.4 (23)	45.3 (24)	39.6 (21)
Priming	58.5 (31)	49.1 (26)	41.5 (22)	43.4(22)
Null	9.4 (5)	7.5 (4)	13.2 (7)	17 (9)

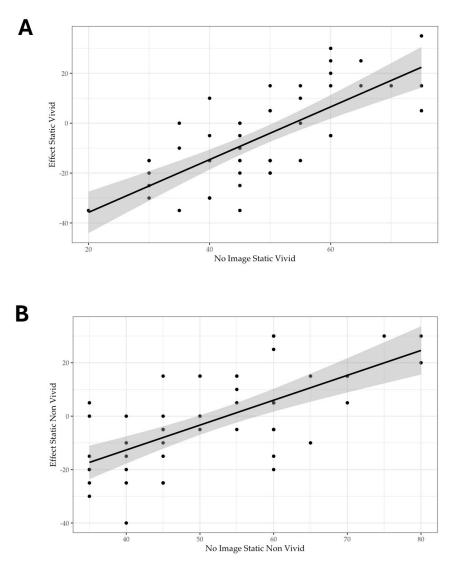
Note. N = 53. Effect Type refers to the resulting score after the NI trials. Negative scores were labeled as priming, including negative Perky effects; positive scores were labeled as interference, including positive Perky effects; and scores of 0 were considered null or no effect. All image types were found to be significant at the p = 0.0001 level. The numbers represent the proportions (%) of participants experiencing the effect, as calculated by N/53 × 100. All the numbers are rounded. The numbers in parentheses represent the number of participants out of N = 53 who experienced each effect for the SV image type (n indicates each image type).

Table 1 outlines the differences observed across mental image types. The largest difference between interference and priming within one image type was 14 participants, with more participants showing priming effects; this was observed for the SV image type (interference: n = 17, priming: n = 31). For SNV images, only 3 additional participants showed priming effects (interference: n = 23, priming: n = 26). For DV images, the difference was 2 participants, with more participants showing interference effects (interference: n = 24, priming: n = 22). For DNV images, 2 additional participants showed priming effects (interference: n = 24, priming: n = 22). For DNV images, 2 additional participants showed priming effects (interference: n = 23).

## 3.2. Positive and Negative Perky Effects

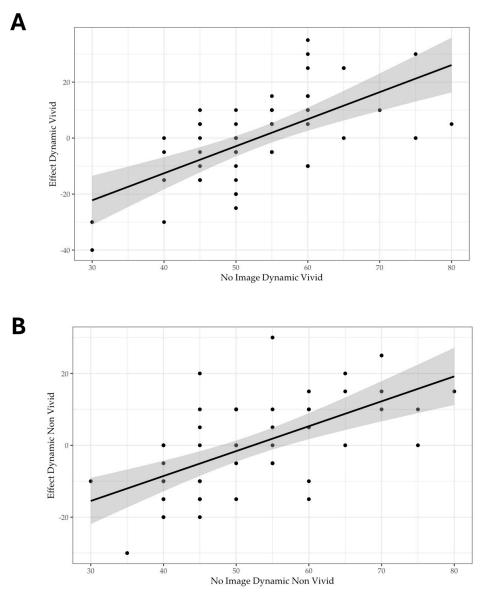
The Mann–Whitney U tests showed significant differences between the positive Perky and negative Perky effects for SV (Z = -5.66, p = 0.000, d = 2.47) and SNV (Z = -5.53, p = 0.000, d = 2.34) images. The results were similar for dynamic images (DV: Z = -5.58, p = 0.000, d = 2.39; DNV: Z = -5.43, p = 0.000, d = 2.24).

We then plotted all the Perky scores for each participant in the static vivid and nonvivid conditions to explain trends based on the image type. These data are presented in Figure 3.



**Figure 3.** Effect of concurrent static imagery on acuity as a function of the baseline Vernier acuity performance for all participants for vivid (**A**) and nonvivid (**B**) images. Gray band indicates 95% confidence interval.

The correlation/regression coefficients for SV ( $r^2 = 0.60$ ; r = 0.78) and SNV ( $r^2 = 0.44$ ; r = 0.66) images showed significant differences between SV and SNV images (t = 2.52, d = 0.49), with a steeper slope for vivid images (i.e., higher interference and priming effects) than for nonvivid images. The same finding was observed for dynamic images: DV ( $r^2 = 0.38$ ; r = 0.62) versus DNV ( $r^2 = 0.36$ ; r = 0.60) (t = 3.62, d = 0.71). The graphs for this analysis are shown in Figure 4.



**Figure 4.** Effect of concurrent dynamic imagery on acuity as a function of the baseline Vernier acuity performance for all participants for vivid (**A**) and nonvivid (**B**) images. Gray band indicates 95% confidence interval.

Further pairwise *t* tests revealed significant differences between SV and DNV images (t = 6.03, d = 1.18) and between SNV and DNV images (t = 3.34, d = 0.66); however, nonsignificant differences were found between SV and DV images (t = 1.96, d = 3.84) and between SNV and DV images (t < 1). This reflects the trend SV > SNV = DV > DNV in terms of the  $r^2$  value. To verify the significance of this pattern, the r coefficients were converted to Zr scores, which were subsequently subjected to polynomial contrast tests. The results confirmed that the trend SV > SNV = DV > DNV was reliable (t(51) = 3.38; *p* = 0.0014, d = 0.66). This finding suggested that there was a clear difference related to vividness, but

there was some overlap between the effects of static and dynamic imagery. To determine the overall pattern, we next examined the possible confounding role of the size of V1.

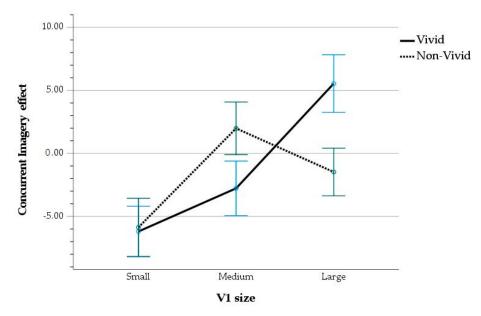
#### 3.3. Priming/Negative Perky Effects vs. Interference/Positive Perky Effects as a Function of V1 Size

In this analysis, we rescaled the effect using the average NI score subtracted from each condition separately (ISV, IDV, ISNV, and IDNV) since we assumed that the baseline remained the same for each subject (we did not find repeated measures of significant changes in NI across the blocks). The three-way V1 size x vividness x static/dynamic ANOVA showed that the only significant interaction with V1 size was vividness (see results in Table 2). The interaction can be analyzed according to Figure 5, which graphically represents the ANOVA results. Individuals with medium V1 sizes experienced modest interference with nonvivid images but priming with vivid images. In comparison, individuals with large V1s experienced priming and negative Perky effects with nonvivid images and interference and positive Perky effects with vivid images, while individuals with small V1s experienced priming irrespective of the vividness of the image (Figure 5).

**Table 2.** ANOVA results, showing the effects of concurrent imagery on Vernier acuity as a function of vividness and V1 size.

Source	Type III Sum of Squares	Df	Mean Square	F	p	Partial Eta Squared
Corrected Model	4319.311 <sup>a</sup>	12	359.943	2.405	0.006	0.127
Intercept	772.346	1	772.346	5.161	0.024	0.025
Vividness	419.980	1	419.980	2.806	0.095	0.014
Static/dynamic	4.871	1	4.871	0.033	0.857	0.000
Subject covariate	20.567	1	20.567	0.137	0.711	0.001
V1 size	2242.093	2	1121.047	7.491	< 0.001	0.070
Static/dynamic X Vividness	70.489	1	70.489	0.471	0.493	0.002
Static/dynamic X V1 size	230.724	2	115.362	0.771	0.464	0.008
Vividness X V1 size	1192.185	2	596.093	3.983	0.020	0.038
Static/dynamic X Vividness X V1 size	21.749	2	10.875	0.073	0.930	0.001
Error	29,780.807	199	149.652			
Total	34,781.250	212				
Corrected Total	34,100.118	211				

$$a R^2 = 0.127$$



**Figure 5.** Effect of concurrent imagery on baseline visual acuity performance as a function of vividness and V1 size. Error bars represent standard errors. The data shown are controlled for subject covariates. Dots and bars in blue and green colors highlight data and standard errors for vivid and nonvivid V1 size categories, respectively.

# 4. Discussion

## 4.1. Summary of Findings and Interpretative Framework

In summary, we found that visual imagery can have priming and interference effects on visual perception depending on differences in individual neuroanatomy (i.e., V1 size). These findings are consistent with our original hypothesis that individual variability in V1 size may influence acuity precision, as V1 biases the differential activation of dorsal and ventral visual streams by directing the streams toward complementary cooperative or competitive interactions. In addition to the influence of V1 size, image vividness modulated perceptual acuity precision. More specifically, our results demonstrated that participants experienced interference, priming, Perky, and null effects across all the image types. Moreover, the priming and interference effects changed as a function of vividness, regardless of the image content (static vs. dynamic). Image vividness acted as a predictor of acuity performance, as reflected by the fact that the four imagery conditions interfered with perception according to our original hypothesis (see Figure 1). Specifically, the more vivid the imagery is, the more interference in the perception. Overall, our results replicate the findings of Reeves et al. [17] and are consistent with the classic "dipper" effect.

The trend of the imagery effects is compatible with classic theories in the experimental and cognitive psychology literature that suggest a functional equivalence between imagery and perception [26,33]. Specifically, adding mental imagery to a visual acuity task reduces the sensory and cognitive resources available for perception, particularly because the process of generating a visual image is related to the process of perceiving a visual image [24,33]. In other words, different image types can influence the working memory load imposed on perception by top-down mental image processing during concurrent imagery-perception tasks. Thus, images affect individuals' perception based on (1) sensory-based working memory capacity and (2) single processing pathways for imagery and perception. If perception and imagery share a common processing pathway and individuals are instructed to simultaneously use visual perception and visual imagery, the two processes must be balanced to achieve optimal performance. Furthermore, both tasks are governed by working memory and higher-order processes. Therefore, the extent to which perception and imagery processing are equilibrated, as well as the imposed working memory load distribution, largely determine the effect of concurrent imagery on perception. Thus, equilibrium between imagery and perception would be reflected by null effects, disequilibrium in favor of perception would be reflected by priming or negative Perky effects, and disequilibrium in favor of imagery would be reflected by interference or positive Perky effects. Thus, the vividness of mental imagery and the size of V1 can individually or jointly improve or reduce an individual's processing ability by priming or interfering with the perception of visual stimuli.

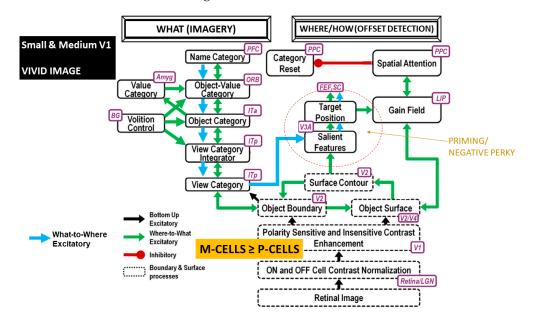
Here, what we refer to as resource competition and equilibrium can be related to Grossberg's ART logic. Namely, feature-category resonance involves the complementary integration of attended features and activated categories related to an object. Resources are reduced when, in the underlying neural networks, the weights of the connections are being learned during the dual task. Direct evidence and conceptualization of this process have been provided in a landmark study by Craver-Lemley and Reeves [34].

We clarify that Grossberg's conceptualization of imagery does not implicate a necessary role of V1. According to Grossberg, imagery is a "volitionally-mediated shift" that "enables top-down expectations, in the absence of supportive bottom-up inputs, to cause conscious experiences of imagery and inner speech, and thereby to enable fantasy and planning activities to occur". In addition, in certain conditions, tonically hyperexcited expectations can lead to conscious experiences in the absence of bottom-up inputs and volition. However, although "both bottom-up activation of visual percepts and top-down cognitively-activated and volitionally-modulated imagery are possible within the visual system" [12], visual representations underlying imagery are formed through hierarchical and interstream interactions in areas V2 to V4, and the final constructed and phenomenologically perceived visual representations are formed in V4 [12]. Imagery, conceived as "top-down expectations plus attention", operates across this hierarchy, thereby reorganizing bottom-level properties [12].

Furthermore, Grossberg argued that, only in some instances imagery should "have effects that are equivalent to bottom-up activation by visual scenes". This argument is supported with the example of imagery of bi-stable patterns (i.e., Necker cube) which should be already biased by top-down expectation and imagined according to one interpretation. We suggest that vividness influences the strength of resonance and individual differences, which, as shown by the literature, could involve resonance loops between the PFC and V1 and be linked to the bottom-up biasing of *spatial* attention (position of a target) without directly influencing bottom-up sensory or low-level effects. Thus, V1 involvement could be linked to the vividness of the level of consciousness or the level of resonance between complementary processes related to the mental image but not the content of the image (in the present context, static or dynamic), as has been recently shown for other features (i.e., object shape) in priming experiments [18]. Thus, activation of V1 during image-related tasks could be the result of top-down reentrant pathways such as indirect PCF feedback to A17 and A18 via A7 [35,36]. The resulting effects of these interactions could be observed in the what-to-where visual stream of processing, where "knowledge" of the features of an imagined object, i.e., the object shroud, influences the detection of a spatial bottom-up sensory target, as in our Vernier acuity task with concurrent imagery.

## 4.2. ARTSCAN Modeling of the Findings

In this section, we apply Grossberg's ART and, more specifically, its related ARTSCAN implementation [37,38] to explain the present findings with a descriptive graphical model. The outcomes of our task can be described in terms of the interactions between the what-to-where and where-to-what parallel processing streams, and these interactions can be examined by considering each of the cases corresponding to the V1 size (3)  $\times$  vividness (2) factorial analysis (see Figure 5). The cases of vivid mental images with small and medium V1s, shown in Figure 6, can be considered together because the only critical difference is the extent to which parvocellular (P-cells) and magnocellular (M-cells) neuronal pools are recruited. In the small V1 case, more M-cells than P-cells are activated. In contrast, for the medium V1 case, the activation of both pools should be approximately equal. This is the "combo" scenario modeled in Figure 6.



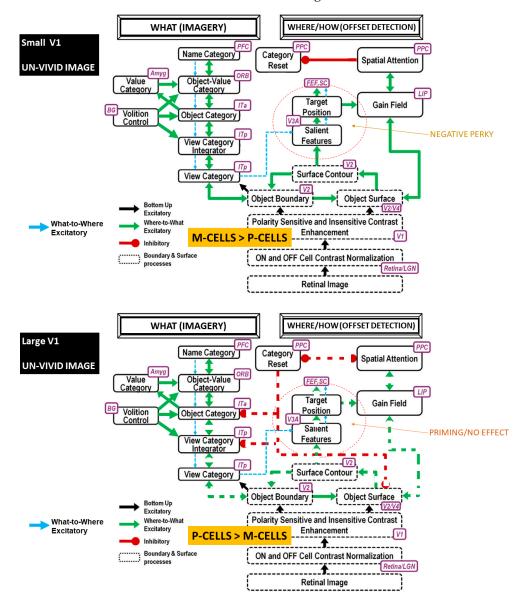
**Figure 6.** An ARTSCAN interpretation of the processes underlying the interaction between concurrent imagery and Vernier acuity line offset detection in the scenario where the observer has small or medium V1 and vivid imagery.

For the case of a small V1 with vivid imagery, the activation of M-cells largely exceeds that of P-cells. Thus, processing is biased toward the spatial pathway. This bias inhibits category reset according to the established attentional distribution. Because of the high vividness, however, the object characteristics are very and equally strong. The size of V1 is associated with the differential activity distribution of the M- and P-cell density. The cell density is directly related to the weight of excitation between and within the what and where/how streams. With a small or medium V1, due to the decreased density of P-cells, the focus is the object boundary of the mental image. Because of the perception of the image boundary and the contour in the periphery, in the small V1 case, or a weaker contour, in the medium V1 case, the object is perceived as fully transparent and/or in the background plane; therefore, the category or knowledge features of the imagined object receive more attention. With high vividness, the what stream is fully excited from bottomup PCF recruitment, but it does not interfere with the where/how stream; in contrast, as the attentional distribution is biased toward the area of the possible target position, the image basically provides a background to better detect the gap between the offset lines. Thus, in the case of vivid images with small and medium V1s, spatial attention is strongly primed by two complementary excitatory influences from interacting systems in V3 and the frontal eye field (FEF). The M-cells allow for strong establishment of the mental image and inhibit the category reset mechanism in the posterior parietal cortex, shifting attention to the category features. The what stream focuses on the imagery present to "fill in" the gap in the spatial features. Thus, the target position is attended to. Without the category reset inhibitory action, the two systems remain complementary, and medium to strong priming (negative Perky effects) occurs.

The case of small V1 and nonvivid imagery, shown in the top panel of Figure 7, is similar to the case illustrated in Figure 6, except that the excitatory connections from the image are weaker than those in the case of high vividness. As a result, the imagined object is perceived as a faint background and receives less attention, which is firmly directed to the area containing the gap in the offset lines, leading to strong priming (negative Perky effects). In contrast, in the scenario depicted in the bottom panel of Figure 7, in which an individual has lower vividness but a large V1, the significant change is the predominant excitation of P-cell activity. This situation induces partial and weak activation of the inhibitory pathway linked with the category reset system since the object is relatively weak. Under these conditions, the object is in focus, and other images do not compete with the image through occluding surfaces. Therefore, in the low vividness condition, the brain focuses on the object boundary rather than the object surface. Imagery then facilitates the detection of the flashed line to "fill in" the boundary. The what stream is the dominant pathway due to P-cell excitation, and ultimately, this pathway is only weakly inhibited by the category reset mechanism. Although the attentional distribution should not be considerably altered, the extent of priming is much weaker than in the above cases, and priming may not occur.

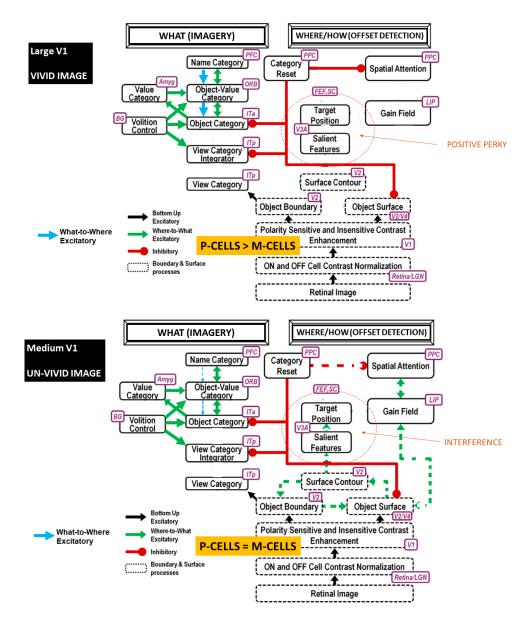
In the large V1 condition with high vividness, as illustrated in the top panel of Figure 8, there is a greater density of P-cells than M-cells. With high image vividness, the brain focuses on the object rather than allowing interference from a competing perceived contour. This induces a discrepancy because more attention is removed from the possible target position and moved to the object, which triggers the where/how system to initiate the category reset mechanism and shift the spatial attention to stabilize perception. However, the boundary and surface of the mental image are both attended to since the object shroud is strong (due to high vividness). Phenomenologically, the image is no longer transparent due to competition between spatial attention and focusing on object category features; therefore, knowledge of its feature contents is similar to amodal perception, with a foreground surface occluding the area where the target and the offset gap appear. The latter results in strong interference in the perception and detection of the target (positive Perky effect). In the related scenario of medium-size V1 and nonvivid imagery, shown in the bottom panel of Figure 8, the density of P- and M-cells is the same, leading to equilibrium between the what and where/how streams. The size of V1 influences the density of P- and M-cells,

impacting the bias or equilibrium between the what and where/how streams. Since there is bias toward the where stream in the low vividness case, the category reset mechanism is activated. The equal density of the P- and M-cells inhibits spatial attention, and the visual mental image is associated with a weak object shroud. This situation induces partial and weak activation of the inhibitory pathway linked with the category reset system since the stability and knowledge of the object are undermined. Under these conditions, the object is in focus amodally, and no other images compete with it on an occluding opaque surface. This leads to interference in the detection of the target.



**Figure 7.** An ARTSCAN interpretation of the processes underlying the interaction between concurrent imagery and Vernier acuity line offset detection in two scenarios in which the observer has nonvivid imagery and either small V1 (**top** panel) or large V1 (**bottom** panel).

In summary, the two key factors that influence imagery–perception interactions are the equilibrium between the strength of resonance in the what system, which determines the extent to which the imagined object is phenomenologically "present" as evident conscious knowledge, and the stable activation of attention toward a spatial target through the control system guided by the object category reset mechanism. Table 3 describes in detail the 7 features that determine the different results.



**Figure 8.** An ARTSCAN interpretation of the processes underlying the interaction between concurrent imagery and Vernier acuity line offset detection in two scenarios in which the observer has nonvivid imagery and either large V1 (**top** panel) or medium V1 (**bottom** panel).

**Table 3.** Summary of the key aspects of the complementary where-to-what and what-to-where pathways in the present experiment.

V1 Size $ imes$ Vividness	Interacting Processes		
Small V1, Vivid(see Figure 6)	<ul> <li>M-cells &gt; P-cells</li> <li>Object shroud strong</li> <li>Spatial shroud strong</li> <li>Object category reset mechanism inhibited by the spatial shroud</li> <li>Strong excitation at the target position</li> <li>Visual phenomenology: object image boundary as background surface</li> <li>Behavioral outcome: negative Perky (strong priming)</li> </ul>		
Medium V1, Vivid(see Figure 6)	<ul> <li>M-cells = P-cells</li> <li>Object shroud strong</li> <li>Spatial shroud moderate</li> <li>Object category reset mechanism inhibited by the spatial shroud</li> <li>Strong what and moderate where excitation at the target position</li> <li>Visual phenomenology: object image boundary as transparent or background, peripheral field</li> <li>Behavioral outcome: variable priming</li> </ul>		

# Table 3. Cont.

V1 Size $\times$ Vividness	Interacting Processes
Large V1, Vivid (see Figure 8, Top Panel)	<ul> <li>M-cells &lt; P-cells</li> <li>Object shroud strong</li> <li>Spatial shroud weak</li> <li>Object category reset mechanism inhibits what excitation to target position and spatial shroud</li> <li>No excitation at the target position</li> <li>Visual phenomenology: object image contour as occluding modal foreground surface</li> <li>Behavioral outcome: positive Perky (strong interference)</li> </ul>
Small V1, Non-Vivid (see Figure 7, Top Panel)	<ul> <li>M-cells &gt; P-cells</li> <li>Object shroud weak</li> <li>Spatial shroud strong</li> <li>Object category reset mechanism inhibited by the spatial shroud</li> <li>Weak what and strong where excitation at the target position</li> <li>Visual phenomenology: object boundary as amodal background</li> <li>Behavioral outcome: variable priming</li> </ul>
Medium V1, Non-Vivid (see Figure 8, Bottom Panel)	<ul> <li>M-cells = P-cells</li> <li>Object shroud weak</li> <li>Spatial shroud moderate</li> <li>Object category reset mechanism inhibited by the spatial shroud and partially by Object Shroud</li> <li>Weak where excitation to target position</li> <li>Visual phenomenology: Amodal perception a foreground surface</li> <li>Behavioral outcome: variable interference</li> </ul>
Large V1, Non-Vivid (see Figure 7, Bottom Panel)	<ul> <li>M-cells &lt; P-cells</li> <li>Object shroud weak</li> <li>Spatial shroud weak</li> <li>Object category reset mechanism partially inhibits what excitation to target position and spatial shroud</li> <li>Weak what and where excitation at the target position</li> <li>Visual phenomenology: object image boundary as amodal background</li> <li>Behavioral outcome: priming or no effect</li> </ul>

#### 4.3. Contributions of Present Work

#### 4.3.1. The Primacy of Complementary Visual Cortical Streams

It is widely accepted that the dorsal visual processing stream is recruited for spatial perception (determining where an object is located), while the ventral stream is recruited for object perception (identifying what an object is) [39,40]. Since the dorsal nervous system determines the positions of visual stimuli in space, we suggest that this pathway is also involved in generating externally projected mental images (placing imagined images in particular spatial locations). Moreover, we theorize that the dual processing involved in detecting visual stimuli and externally projecting mental images may be responsible for creating interference (positive Perky effect) when detecting visual stimuli. Furthermore, given the role of the ventral visual system in object recognition, i.e., categorization, ventrally dominant individuals receive less interference from concurrent imagery, as ventral mediated imagery does not directly compete with the resources necessary for accurate perception of visual details in the external environment.

In agreement with Grossberg's theory, the "what" and "where/how" cortical streams seem to interact to determine the vividness and perception of visual objects. We observed that visual acuity scores were dependent on an individual's V1 size and vivid imagery ability. This influences the recruitment of the dorsal and ventral visual pathways. The involvement of the dorsal and ventral pathways determines whether the imagery is more sensory/category oriented or more detail oriented. Grossberg [25] described how visual cortical areas such as V1 enable our brains to consciously see. The ventral (what) and dorsal (where/how) streams interact through bottom-up, horizontal, and top-down interactions [25]. Top-down interactions use object and spatial attentional processes to engage consciousness. Top-down attentive matching creates synchronous resonant states that lead to bottom-up recognition of categories and top-down expectations [25]. Attentive matching may impact both mostly conscious (object shroud) and mostly unconscious (spatial shroud) seeing.

However, the size of V1 could introduce bias and change the dynamic interaction among the dorsal and ventral areas. As Grossberg [26] described, the architecture of the dorsal and ventral streams and the relationship between the two enables image recognition and determines appropriate actions. Furthermore, without bottom-up data, Grossberg's theory [13] describes how and why top-down interactions can lead to imagery with volitional modulation. Grossberg also suggested that imagery is not only an entity itself but also part of the complex dynamic system of seeing and thinking. In other words, in Grossberg's theoretical infrastructure, imagery is an important component in vision and thinking. Thus, imagery findings impact perception, and knowledge regarding perception can be applied to imagery. The vividness of an experience in the visual field, including light, color, and extra sensory information, draws human attention and necessarily activates both the ventral and dorsal streams. Within this system, we attempted to clarify the possible role of V1 through indirect measurements and suggested vividness as a possible bias guiding perception and imagery. Moreover, the novel aspect of this paper is the contribution and analysis of the role of V1. V1 is a high-level interaction region with the ventral and dorsal streams. An individual's V1 size may influence the individual's bias toward the dorsal or ventral stream through the reentrant loop. This would potentially contribute to reconcile why V1 activation during visual imagery is a ubiquitous find (e.g., in fMRI studies). Indeed, it should be expected that only imagery situations that induce extreme disequilibrium between dorsal and ventral processes in certain individuals (hence, usually a proportion of the sample) should reveal strong and clear evidence of V1 activation (or deactivation).

Kosslyn provided extensive independent supporting evidence demonstrating the importance of the dorsal and ventral pathways, as described in [40], and D'Angiulli and Reeves [28] described how vividness ratings reflect the strengths and weaknesses of the dorsal and ventral pathways. The vividness (or image strength) ratings and image latency could represent the combined action of the two pathways and their roles in both imagery and perception [6]. These two pathways are core mechanisms involved in image generation and high-level vision tasks that keep being rediscovered in current imagery research (see [19,41]), but no detailed model of their emerging dynamics has been previously proposed.

Although the role of the dorsal and ventral pathways has been described in the literature, the bias of V1 toward the dorsal or ventral pathway is another novel contribution of the present study. Importantly, we do not make any assumptions about the bias toward the dorsal or ventral streams, and we suggest that external bias, task demands, and individual differences (including V1 differences) impact responses to perceptual stimuli. What we call "voluntary" (for example, our unconscious bias) is a complex system of interactions. Rather than voluntary, this intertwining nature is autonomous in attending, categorizing, recognizing, and predicting objects, which is central to Grossberg's ART and the idea of the resonant brain. Our contribution emphasizes the primacy of the link among V1, the dorsal and ventral pathways, and visual phenomenology [12].

## 4.3.2. Limitations and Future Research Directions

In this context, a limitation of this work, and the literature, is the lack of understanding of exactly how attention affects unconscious and conscious bias toward the ventral and dorsal pathways. Future research should therefore focus on conscious and unconscious bias and how attention is linked to V1 and the dorsal and ventral pathways. Overall, the interaction among the dorsal and ventral pathways, vividness, and the size of V1 could improve our understanding of how individual differences in perception (sometimes major differences with influential consequences) occur. This understanding might be useful in educational applications. In particular, imagery training is a key application for this research. For example, young children with less acuity (who are cognitively less attentive to external stimuli) could benefit from imagery training. In this paper, we found that image vividness affects the perception of external stimuli. Generating imagery could lead to stronger priming of perceptual processing. More importantly, training and practice could be determined according to individual characteristics and task types, as some children

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may suffer unwanted interference and divided attention or distraction due to images that are too vivid. Similar applications could be considered for clinical, mental health, and psychotherapy settings, which routinely use mental imagery training and practice.

Some limitations of this paper include the relatively small sample size and the limited diversity of the participants. A larger, more diverse demographic would add more varied V1 size data as well as different imagery abilities. In light of these limitations, the interpretations and data are preliminary and should be considered an attempt to examine the impact of individual differences and phenomenology on dynamics that extends imagery research.

Our contribution should be considered a hypothetical extension of ART for future neurophysiological work on imagery and imagination. As mentioned, the present study is merely descriptive and limited to replicating Kosslyn's data and Grossberg's insights; however, connecting subjective and phenomenal results to actual empirical neural dynamics remains challenging. Ongoing investigations in our laboratory aim to extend the proposed framework using combined fMRI, EEG, and ERP techniques and deep learning simulations. We hope to elucidate the groundbreaking contributions of Grossberg's ART. The proposed approach might permit the prediction of phenomenology and subjectivity and individual differences starting from emerging complex properties of neural networks, in contrast to the large majority of research that, up to now, has proceeded in the opposite direction, going from insights driven from phenomenology and introspection to experimental phenomena and to cognitive and neural architectures (see [42,43]). The present proposed approach may considerably improve the current state-of-the-art in top-down attention, imagery, and consciousness research. In the most practical sense, the identification of the different possible scenarios of complex neural interactions between perception and imagery (as analyzed in Figures 6–8) and the reduction to a manageable set of system variables (as illustrated in Table 3) provide a testable and falsifiable computational working model of vividness which is amenable to further empirical and theoretical refinements, moving the bench from introspection to manipulation of objective variables within interacting complex systems, especially in terms validating implementations based on neural networks simulations. A far-reaching objective is that, through the advancement of multidisciplinary meta-theory, the present conceptualization of vividness might, in future research, be abstracted and generalized further, from the level of human domain to neuromorphic computing and neurorobotics to arrive at possible new forms of autonomous machine explainability (for more in-depth discussions see [2]).

#### 5. Conclusions

In conclusion, we showed that concurrent imagery can exert interference, priming, or no effects on perception depending on the interaction between image vividness and individual differences in neuroanatomy, including dynamic complementary parallel processing in ventral and dorsal visual streams. Our results suggest that highly vivid images and large (ventrally dominant) V1 interfere with perception, whereas weak imagery and small V1 (dorsally dominant) prime perception. A possible interpretation is that the size of V1 affects the neural synchronization between the connectivity of this region and other dorsal and ventral regions according to reentrant feedback from the PCF, thereby also influencing the vividness of the perception. Hence, under our static vivid imagery condition, the interference effects are greater than those under the static nonvivid and dynamic vivid conditions and more than double the effect than that under the dynamic nonvivid imagery condition.

Overall, we conclude that in most situations, imagery enhances perception, possibly because mental images are often processed by ventral pathways. The ventral network is beneficial for perception during imagery tasks because this network carries information that is less likely to compete with working memory and the attentional systems necessary for accurate visual-spatial prediction in the where/how system. However, despite these findings, there is still large individual variation among individuals, which appears to be due to the vividness of the image and the relative cortical size of the V1 area.

Our interpretation of ART and related descriptive modeling based on ARTSCAN contributes to expanding Grossberg's comprehensive account of how and why individually experienced vividness may influence the differential use of the dorsal and ventral complementary visual processing pathways, resulting in the reported effects of imagery on concurrent perception.

**Author Contributions:** Conceptualization, A.D.; methodology, A.D.; validation, C.L. and D.M.B.; formal analysis, A.D. and D.M.B.; investigation, A.D.; data curation, A.D. and D.M.B.; writing—original draft preparation, A.D., C.L. and D.M.B.; writing—review and editing, A.D.; supervision, A.D.; project administration, A.D. All authors have read and agreed to the published version of the manuscript.

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**Institutional Review Board Statement:** The study was conducted in accordance with the Declaration of Helsinki, and approved by the Institutional Behavioural Research Ethics Board of Carleton University (protocol code 111569 27 November 2019).

Informed Consent Statement: Informed consent was obtained from all subjects involved in the study.

**Data Availability Statement:** The data presented in this study are available upon request from the corresponding author. The data are not publicly available because open data sharing was not included as an option for consent.

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