

DOI: https://doi.org/10.1093/nc/niaf026

Research Article

Vivid imagery of objects primes perception of subliminal spatial information

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Abstract

The integration of imagination with perception of reality is associated with numerous neurocognitive and biological adaptive functions. Given the overlap between neural processes and regions governing internally versus externally generated imagery, the interaction between these processual components of high-level vision has been studied for over a century, without yielding a satisfactory account. Opposite to traditional theories like the Perky effect or sensory boost, we hypothesized that voluntary conscious mental imagery of an object enhances the processing of unconscious incoming visual spatial information. Hence, aspects of internal imagery such as vividness or motion should drive such an interaction. We probed how subliminal spatial information might be influenced under imagery conditions. Using behavioural data, we show that imagery improves the unconscious concurrent perception of visual spatial information. This priming effect seems driven by the gradient of imagery vividness: both explicitly required by task demands and implicitly generated. We found that imagery can direct visual perception when the visual system is strongly biased towards predicting that an object is present. Because the observed results vary systematically with self-reported vividness, rather than being epiphenomenal, the subjective experience of vividness is a deterministic condition for imagery priming.

Keywords: visual mental imagery; visuo-spatial perception; awareness; subliminal processing; vividness; visual acuity; Default Mode Netwrok (DMN); visual processing streams; externalization (out-of-body)

Introduction

Throughout each day, humans process their surroundings and interactions in both conscious and unconscious streams (Bargh and Morsella 2008; Su et al. 2016). Driven by senses, one primary contributor of information to these processes is the near-constant stream of visual information (van Gaal and Lamme 2012). Visual information is processed in a series of brain regions beginning with geniculostriate and tectopulvinar pathways and on to the visual cortex and occipital lobe (Westwood 2009). Visual information entails more than the light coming in, and indeed our imaginations allow us to represent our own version or simulation of vision in the form of imagination and imagery (Currie 1995). The origins of such imaginations have been the subject of continued centuries old debate in philosophy and science, which ultimately led to the contemporary synthesis that a widely distributed network of visual areas in the occipital, parietal, and temporal cortex contribute to modality-specific and multimodal imagery (Farah 1989). While many evolutionary and philosophical questions persist surrounding the purpose and essence of internal imagery or imagination, other researchers began asking questions about its 'realness'. Specifically, how real are these images? And

how might they compare to the ones experienced through perception, as opposed to those generated from within (see review and discussion in D'Angiulli and Roy 2024).

One of the earliest descriptions of the essential evaluation of internal and external imagery which gained substantial fame was the Perky effect (Perky 1910; Segal and Gordon 1969; Segal and Fusella 1970). In essence, it was observed that real objects could be perceived as being imagined, and taken further, that this imagery interferes with real perception (Segal and Fusella 1970). The classical interpretation of this effect follows that during imagining of visual imagery, co-activation of brain regions governing the processing of both 'real' and 'imagined' visual information become somewhat indistinguishable, obscuring conscious understanding of the 'real' external information being presented (Craver-Lemley and Reeves 1992; Craver-Lemley et al. 2010; Reeves et al. 2020; Dijkstra & Fleming, 2023).

Visual imagery is associated with activation of the ventral temporal, lateral occipitotemporal, and posterior frontal cortices (Fulford et al. 2018; Alho et al. 2023), and during simultaneous visual and imagery conditions these representations are shown to be disrupted, indicating that the encoding of visual objects, regardless

of their external or internal origin, share neural space (Alho et al. 2023). Thus, the theory of interference ruled out numerous alternative explanations or contributors to the effect, and garnering a substantial body of behavioural evidence (Reeves and Segal 1973; Craver-Lemley and Reeves 1987, 1992; Craver-Lemley et al. 1997).

The coalescing characteristics of the imagery and the real object pose an unaddressed problem however: the instances in which imagery interferes with real object perception may be only true in a circumscribed set of conditions. There is abundant evidence of many conditions in which the opposite is true, i.e. concurrent visual mental imagery facilitates, or primes perception as opposed to preventing or obscuring its processing (a topic reviewed extensively elsewhere, Pearson 2019).

Imagery is also not simply just a mental project of an image with finite quality and characteristics. Most individuals can manipulate and control their imagination, selecting mental imagery which varies in brightness, clarity, intensity, valence, and movement (Marks 1973b; D'Angiulli et al. 2013; Syed et al. 2020). Indeed vividness has a substantial contribution to the recall and overall representation of mental object, not only highlighting its commonplace role in the generation of imagery, but also suggesting its influence over competing perceptual processes in Perky-type situations (Marks 1973b; D'Angiulli and Reeves 2007; D'Angiulli et al. 2013). If vividness contributes to better recall and instigates imagery's long-term accessibility, we argue that its contribution to the generation of imagery and its subsequent effect on visual perception also require objective quantification.

Our hypothesis, which opposes traditional conjecture surrounding the effect of imagery on visual perception, follows that in cross-genre settings (i.e. where visual imagery is not acquainted with the presented visual stimulus) and further in instances where visual stimuli are below conscious perception, vivid imagery would instead trigger the activation of the whatto-where/how visual streams of complementary processing (Grossberg 2021), thereby priming relevant brain regions which support the automatic search for an object in space (Freeman 1983), thereby resulting in enhanced visuo-spatial ability. If true, we would also expect that this level of priming would be contingent on both the vividness of the imagery (as a function of intrinsic DMN-visual area engagement), and the individuallevel ability to generate imagery. Specifically, high imaginers with greater trial-level vividness scores would show evidence of priming, while low imaginers with respectively lower triallevel vividness may not. Here, we refer to trial-based vividness as a specific processing individual ability linked to learning and episodic memory and associated with expertise in the context of a particular retrieval demand (Kosslyn et al. 1984; Runge et al. 2015), in contrast to general trait-imagery ability linked with declarative memory as measured by the Vividness of Visual Imagery Questionnaire (VVIQ) (Marks 1973b; Runge et al. 2015). This distinction is important as it implies that trial-bytrial vividness can fluctuate significantly depending on context (Reeder 2017) and independently from the VVIQ (Pearson et al. 2011; Dijkstra et al. 2017; Marks 2019).

In the current study, we carried out a generalization of Perky's original study, in which participants generate visual imagery under a pre-existing set of contexts. Our goal was to understand how imagery and its characteristics such as vividness and motion can alter perception of real visual stimuli. We measured the ability of individuals to detect subliminal visual stimuli under imagery and non-imagery conditions, while accounting for their own reported ability to generate vivid imagery. In doing so, we hoped to uncover how imagery, and its associated quality of vividness, might bias the perception of real visual information delivered below a perceptual threshold. Specifically, following our hypothesis, we predicted that trial-based vivid imagery would prime subliminal visual acuity.

Materials and methods

Participants

Sixty first-year undergraduate psychology students aged 18 to 25 years (M=22, SD=1.75) were recruited to participate from Carleton University. The inclusion criteria required that the participants had never completed a mental imagery experiment previously and had signed a written informed consent form. The Institutional Behavioural Research Ethics Board of Carleton University approved this study (protocol #11156927), which was conducted in accordance with the Declaration of Helsinki and Canada's Tri-Council Policy Statement.

All participants were part of a prospective cohort study with several follow up imagery conditions, this was the first imagery experiment the participants completed; data on the other conditions are included in other successive cohort-study reports (see D'Angiulli, Laarakker & Buchanan 2024). Fifty-three per cent of participants identified as male and 47% identified as female.

Screening and exclusion

In the preliminary phase of the study, the participants underwent personality and imagery screening using the VVIO (Marks 1973a) and the Big Five Inventory (John et al. 1991). VVIQ was used as a screening measure to ensure participants were capable of mental imagery.

Following the standard procedure, the participants were presented with the 16 VVIQ descriptions and asked to generate and then rate the experienced mental images on a scale of 1 (perfectly clear) to 7 (no image). Participants who scored within the typical range (within 2 SD of the grand mean) in both questionnaires were included in the present study. Seven candidates scored below the norm on one of the items in the Big Five Inventory; and were excluded. Participants also filled out a questionnaire detailing frequency and use of drugs, alcohol, and medications, which was a criterion for exclusion. After screening, 53 participants were included.

Experimental design

The experiment followed a within-subject design where the same observer served as their own control in a series of repeated measures conditions involving spatial perception and imagery or spatial perception only (no image generation). The study design was based on a series of perception studies which probed how imagery alters perception (Craver-Lemley and Reeves 1987; Craver-Lemley et al. 1997; Craver-Lemley et al. 2010; D'Angiulli et al. 2021).

Participants completed questionnaires gauging task and context-specific vividness and mental imagery generation capability: the Test of Static and Dynamic Visual Imagination (TSDVI), and self-reported speed of imagery (D'Angiulli et al. 2013). In contrast to the VVIQ, these questionnaires probe trialbased vividness, not trait-based imagery ability, thus these by-trial measures are more reliable than VVIQ in capturing task related changes in imagery vividness (Runge et al. 2017) and more specifically probe the vividness of the produced imagery.

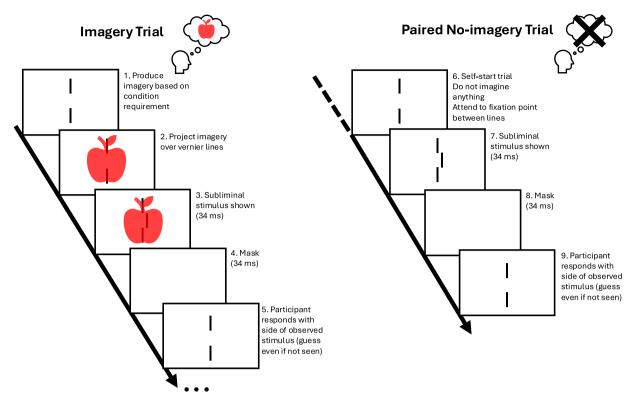


Figure 1. Schematic of task demands and imagery/no-imagery trials.

Visual (vernier) acuity task

Following explanation of the task requirements, participants were presented with an adapted visual acuity task used previously (Craver-Lemley and Reeves 1992). Participants were asked to observe a visual projection of two vertical lines, 1.2 m and 2.6° visual angle downward from the individual, using a Sony Duocom LCD Data projector. The two lines (each 5 mm) were presented above on another, separated by a space of 5.84 cm. A third line (the subliminal stimulus) was presented either to the left or right of the blank space at 0.2 mm. The line was presented for 34 ms, after which the screen was masked for 34 ms. This duration falls on the low end of the window of subliminal perception, between 30 and 150 ms (Sandberg et al. 2022).

After presentation, participants were asked to verbally indicate if they saw something on the left or the right of the two fixation lines, or to make their best guess even if they had not seen anything. Participants were not told which type of visual object was the target. A schematic of the task and conditions is presented in Fig. 1.

Imagery conditions

There were five possible conditions for participants, produced through a combination of vivid/non-vivid and dynamic/static imagery and non-imagery requirements. Each participant first underwent five practise blocks, and was asked to produce one combination (e.g. static and vivid) of imagery. Participants would confirm they had generated the image verbally or non-verbally (e.g. pen click), after which the experiment would begin with the stimulus presentation. Following each imagery trial, participants would attend the display without generating an image (i.e. nonimagery trial) and again be shown the stimulus. There were 16 experiment blocks with 10 trials each, for a total of 160 trials, with even distribution of the four conditions. Accuracy was taken on a conditional basis, thus the portion of correct responses out of total responses per condition.

Importantly, imagery selected for each of the combination of conditions was pre-selected by the participant, and thus the task demands assume the same (within-subject) imagery content is produced for each trial of the same condition type. For vividness, we defined vivid imagery as 'the extent to which the imagined object is lifelike' (D'Angiulli and Reeves 2007). Thus, vivid versus non-vivid imagery was given the example of 'your parent's face versus your preschool teacher's face'. Similarly, static and dynamic imagery was given the example of something not moving (i.e. a park bench) and something moving (i.e. a flag blowing in the wind), respectively (similarly as in the VVIQ protocol). Participants were asked to generate their own examples to use for the experiment. This process is further described in other work (D'Angiulli et al. 2024).

Data analysis

Statistical analyses were carried out in JASP 0.18.3.0. Pearson correlations were used to correlate trial-level measures of vividness and image generation speed. A repeated measures analysis of variance (rmANOVA) was carried out with repeated measure factors of imagery (e.g. imagery or non-imagery condition), vividness (e.g. vivid or non-vivid imagery trial), and movement (e.g. dynamic or static imagery). Between subject factors included TSDVI scores and the perceived vividness scores at the trial level. Both factors were categorized into low, moderate, and high categories of scores distribution (Table 1). In this way, we could investigate the effects of each trial quality, while accounting for individual imagery quality and self-rated vividness, which addresses issues of relative vividness between subjects.

Since we sought to determine the effect of imagery and its quality on priming, we considered analyses which investigate the

Table 1. Perceived vividness and TSDVI category levels with image generation speed.

TSDVI category (n)	Mean TSDVI (SD)	TSDVI range	Mean speed, s (SD)	
Low (17)	1.884 (0.286)	1.321–2.215	2.998 (0.380)	
Medium (17)	2.599 (0.169)	2.321–2.857	2.580 (0.249)	
High (17)	3.576 (0.454)	2.89–4.357	2.353 (0.292)	

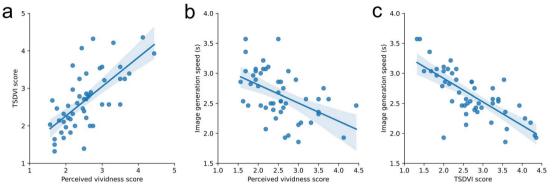


Figure 2. Trial-level vividness and image generation speed. (a) Perceived vividness and TSDVI score. (b) Perceived vividness and image generation speed. (c) TSDVI score and image generation speed. Shaded area denotes 95% CI.

effect of imagery and its characteristics on priming to be planned. In contrast, interactions with individual-level imagery quality and self-rated vividness are therefore considered as exploratory (unplanned). For planned analyses, we based our sample sizes on previous Perky-based experiments, and those investigating subliminal perception. To achieve a medium-large effect sizes, assuming α error probability=.05 and power=.95, as reported in previous works, we determined we needed a median of 15 participants in a vernier acuity task comparing imagery to noimagery (Craver-Lemley et al. 1997), and studies investigating subliminal perception at around 30 ms found significant effects with a median sample size of 24. Thus, looking at an interaction between these effects, our total sample size of 53 participants lends us a sufficient sample size for reliable analysis on both qualities.

We considered P < .05 as a significant effect. Post-hoc testing was Holm corrected for multiple comparisons.

Results

The main results of this study were interpreted from the significant effects and interactions of the rmANOVA. Results are ordered based on the ordered hypotheses and logical narrative, and so main effects and interactions are provided alongside the associated post-hoc analyses.

Trial-level vividness scores and image generation speed

We first examined the relationship between individual measures of vividness including the TSDVI, the speed at which imagery was generated, and the trial-level vividness ratings. All of the measures were highly correlated, with TSDVI score and perceived vividness positively correlated (r = 0.670, P < .001; Fig. 2a), TSDVI and image generation speed negatively correlated (r = -0.739, P < .001; Fig. 2b), and perceived vividness and image generation speed negatively correlated (r = -0.492, P < .001; Fig. 2c).

To estimate the impact of the fluctuation of the trial-based vividness relative to the trait vividness (i.e. as reflected by the

VVIQ), we also correlated trial-level vividness scores and self-reported speed to VVIQ. As expected, the effects were modest, the correlation between perceived vividness, TSDVI and VVIQ, were 0.546 (P=.002) and 0.442 (P=.013), respectively; and the correlation between image speed and VVIQ was -0.347 (P=.055). These findings are consistent with previous literature in that it demonstrates that VVIQ is only partially consistent with trial-level task-specific imagery ability (see meta-analysis in Runge et al. 2017).

Imagery primes subliminal detection

We sought to understand how any type of imagery might alter unconscious detection of a subliminal probe.

We hypothesized that imagery rehearsal trials would enhance detection of a subliminal probe, consistent with the priming theory, particularly compared to control trials in which participants were asked (immediately following an imagery condition) to simply observe the screen and vernier lines without imagery demands.

The rmANOVA revealed a significant effect of imagery on detection accuracy (F(1,42) = 4.257, P = .045, $\eta^2 = 0.011$). The mean accuracy of subliminal stimulus detection during imagery conditions was 53.788% (SE = 1.49%, 95% CI [51.5, 56.08]), while control trials yielded an accuracy of 50.711% (SE = 1.51%, 95% CI [48.39, 53.03]; Fig. 3a). We therefore had initial evidence that repeated imagery evoked in any condition improved probe perception above chance.

Interestingly, the strength of the effect of imagery was further contingent on the quality of the imagery and the rehearsal abilities of the imaginer, as we observed an interaction between imagery condition (e.g. imagery or non-imagery), movement (e.g. dynamic and static imagery), and the category of TSDVI $(F(2,42)=3.490, P=.040, \eta^2=0.015)$.

Post-hoc contrasts revealed a significant difference between the low- and medium-category TSDVI in the dynamic imagery condition (t(42) = 4.053, P_{corr} = 0.014; η^2 = 0.28). Furthermore, during the control trial immediately following the static imagery condition, the medium-category TSDVI participants yielded

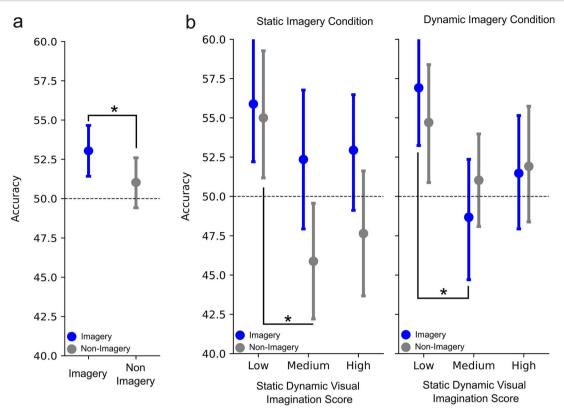


Figure 3. Effect of imagery and TSDVI on the accuracy on subliminal detection. (a) The general effect of imagery on accuracy. (b) The interaction between TSDVI score, imagery movement, and imagery requirement on accuracy of subliminal detection. *P < .05. Dashed line indicates chanceprobability of accuracy. Error bars denote 95% CI.

significantly reduced accuracy compared to the low-category TSDVI (t(42) = 3.81, $P_{corr} = 0.029$, $\eta^2 = 0.257$). Indeed the 95% CI of the medium category did not include 50%, suggesting that the non-imagery condition in medium-category TSDVI participants had an inverse influence (i.e. decrement) on accuracy (Fig. 3b). Across both static and dynamic imagery conditions, the low-TSDVI group accuracy 95% CI did not contain 50%.

Vividness of imagery drives perceptual priming in dynamic conditions

The rmANOVA also revealed a significant interaction across all conditions (imagery, vividness, movement, and TSDVI group; F(2,42) = 6.113, P = .005, $\eta^2 = 0.022$). We first considered the interaction between imagery, vividness, and TSDVI under dynamic conditions.

Post-hoc testing comparing groups between conditions found a significant difference between the medium- and high-TSDVI groups in the dynamic vivid imagery conditions (t(42) = 3.79, $P_{corr} = .007$; $\eta^2 = 0.255$). Interestingly, we also found a marginally insignificant difference between the low and medium groups $(t(42) = 2.77, P = .09, \eta^2 = 0.154)$, hinting that both low and high groups display priming effects in the dynamic, vivid imagery conditions, when compared to the medium-vividness group (Fig. 4). Mean accuracy with SE and confidence intervals are reported in Table 2.

Post-hoc analyses also revealed a marginally significant difference between the low- and high-TSDVI groups in the dynamic non-vivid imagery conditions (t(42) = 3.06, $P_{corr} = 0.049$; $\eta^2 = 0.182$), in which the low-TSDVI group indicated a higher accuracy of subliminal perception (Fig. 3).

Vividness of imagery drives perceptual priming in static conditions

No post-hoc analyses were significant for the static imagery conditions.

Individual qualities of vividness production modulate perceptual priming

The final significant result of the rmANOVA indicated that individual vividness production (i.e. rehearsal) ability had a significant effect on subliminal perceptual accuracy (F(2,42) = 8.574,P < .001, $\eta^2 = 0.059$). Post-hoc testing revealed a significant difference between the low- and medium-TSDVI accuracy $(t(42) = 4.12, P_{corr} < 0.001; \eta^2 = 0.288)$, and low- and high-TSDVI accuracy $(t(42) = 2.616, P_{corr} = 0.025, \eta^2 = 0.140)$. There was no significant difference between the medium- and high-TSDVI accuracy (t(42) = 1.28, $P_{corr} = 0.207$; $\eta^2 = 0.037$; Fig. 5).

Individual qualities of vividness production interact with vivid imagery production and its effect on priming

In the dynamic vivid condition, we observed no significant difference between the low- and high-TSDVI groups, but instead between the low- and medium-TSDVI accuracy (Fig. 4), with an apparent 'dip' in the middle category. We chose to fit a quadratic regression curve to the data to determine if low and high TSDVI possessed similar high accuracy, while medium TSDVI boasted reduced (indeed below 50%) accuracy. The overall model was significant $(F(2,42) = 5.51, P = .006, R^2 = 0.187; Fig. 6a)$.

Conversely, in the dynamic non-vivid imagery condition (Fig. 4), we observed a significant difference between the low- and high-TSDVI. This effect appeared to indicate that while low-TSDVI

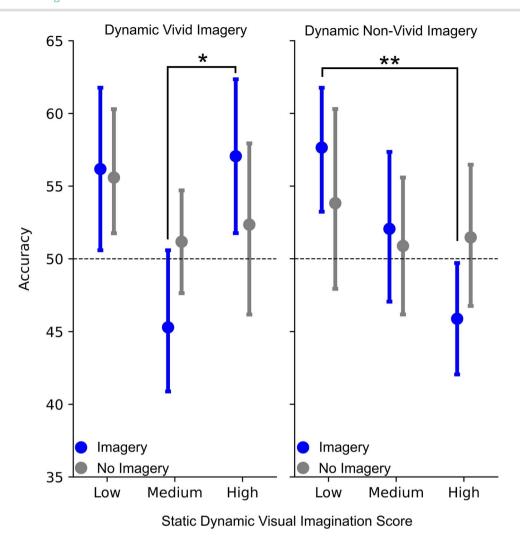


Figure 4. Subliminal perception accuracy under dynamic imagery conditions and subsequent control trials. Error bars indicate 95% CI. *P < .05, **P < .01.

Table 2. Marginal mean accuracy in dynamic conditions and 95% CI.

SDVI group	Vividness	Imagery	Mean accuracy % (SE)	95% CI
Low	Vivid	Imagery	61.25 (3.33)	[54.53, 69.70] ^a
		Non-imagery	57.64 (3.08)	[51.41, 63.86] ^a
	Non-vivid	Imagery	57.92 (3.24)	[51.37, 64.46] ^a
		Non-imagery	50.28 (3.66)	[42.84, 57.67]
Medium	Vivid	Imagery	44.00 (2.80)	[38.37, 49.63] ^a
		Non-imagery	51.85 (2.59)	[46.63, 57.07]
	Non-vivid	Imagery	49.66 (2.72)	[44.18, 55.16]
		Non-imagery	49.22 (3.07)	[43.02, 55.42]
High	Vivid	Imagery	61.25 (3.33)	[54.53, 69.70] ^a
		Non-imagery	46.67 (3.08)	[40.44, 52.89]
	Non-vivid	Imagery	47.50 (3.89)	[40.95, 54.05]
		Non-imagery	52.08 (3.66)	[44.69, 59.48]

^aNinety-five percent CI does not contain 50% chance value.

participants possessed greater-than-chance accuracy of subliminal detection, medium-TSDVI participants did not differ from chance, and high TSDVI interestingly possessed a detection accuracy below chance. We modelled this effect as a linear regression with TSDVI as a factor, and dynamic non-vivid imagery condition accuracy as the outcome. The overall model was significant $(F(2,42) = 5.685, P < .001, R^2 = 0.192; Fig. 6b)$.

Discussion

In this study, we considered how mental imagery might alter the detection of a subliminal probe as a function of vividness and imagined movement. We hypothesized that mental imagery would prime detection of a subliminal stimulus, and our results supported this theory, but only under certain conditions.

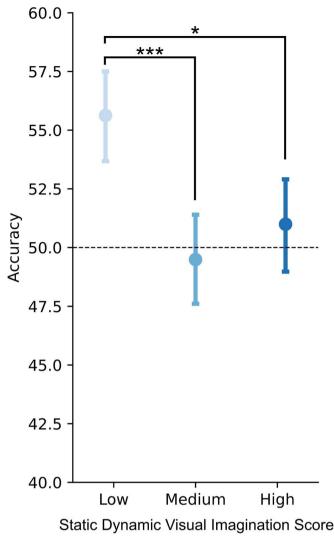


Figure 5. The effect of TSDVI score on overall subliminal perceptual detection. *P < .05, ***P < .001. Error bars depict 95% CI.

We found that globally, imagery trials (of any imagery type) produced greater-than-chance detection of the subliminal stimulus compared to control trials. Interestingly, regardless of whether the imagery was static or dynamic, individuals with a low TSDVI maintained detection accuracy above chance, while medium and high groups did not indicate apparent global priming. Interaction effects clarified this trend further, as we found that during dynamic vivid imagery, both low- and high-TSDVI groups boasted greater-than-chance detection of subliminal stimulus modelled as a parabolic function. In the dynamic non-vivid imagery, however, the trend across TSDVI groups was better described as linear, with low-TSDVI individuals indicating greater accuracy, while medium-TSDVI participants generally performed at chance level. Even more interesting, was a below-chance level of accuracy in the high-TSDVI group only during non-vivid imagery. Overall, TSDVI was generally associated with detection accuracy, with the low-TSDVI group indicating accuracy greater than other groups, and above chance.

These findings contribute to a long history of work on imagery and its influence on perception (e.g. Perky effect), but highlight a novel phenomenon in which, even when the target object is not consciously perceived, vivid imagery can increase unconscious perception by enhancing the intake of spatial information. Indeed,

our results provide possible explanation for the steady rise in results which are inconsistent with the Perky effect, countering traditional theories on down-regulated external information processing during imagining.

Imagery and subliminal detection

Our primary finding, an apparent increase in accuracy during imagery trials, was inconsistent with, and indeed opposed, the previously described Perky effect (Perky 1910; Segal and Gordon 1969; Segal and Fusella 1970; Craver-Lemley et al. 2010; Reeves et al. 2020). Given that our probe was delivered subliminally, we would expect no deviation from chance-level detection if imagery prevented processing of the probe. Importantly, we did not ask participants to imagine the probe itself (if we had, this instead may have been supportive of the Perky effect), but instead the imagery produced was unrelated, and the probe's location was randomized. Our finding was of particular interest, then, as it posited that some aspect of imagery was not interfering with perception, but rather enhancing it.

This proposition is not new, both imagery of colour (Chang et al. 2013) and pattern (Pearson et al. 2008) bias conscious perception of real external visual information, but what is distinct about our

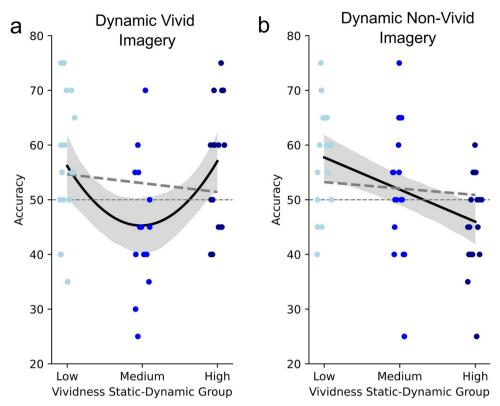


Figure 6. Regression modelling for dynamic imagery conditions: (a) vivid and (b) non-vivid. Solid regression line indicates imagery condition modelling. Dashed line indicates subsequent control trial for contrast. Shaded area represents 95% CI.

approach is that the imagery was not of the same genre as the subsequent external visual cue. It is more comparable to understand how imagery of an object might bias perception of a similar object, much like how pure colour imagery interferes with and influences the perception of a subsequent colour stimulus. Indeed, except for one study (Reeves and Segal 1973), the majority of studies which reported Perky effects using an experimental set up similar to ours requested the observers to imagine contents similar to the targets (straight lines or geometrical patterns containing straight lines). Our finding illustrates that imagery itself appears to prime the visual pathway such that subliminal (and otherwise undetected) stimuli arise into (unconscious) perception. We note that this effect is also primarily spatial, given that the key variable is location, namely, the side of the target lines determining the vernier gap. We can then summarize the effect as being that imagery primes spatial processing of subliminal objects, but with one key factor: individual TSDVI.

Individual imagery abilities and the priming effect

A consistent pattern across our findings was that the low-TSDVI group generally performed better, boasting higher accuracy during vivid and non-vivid imagery trials (Fig. 6), and generally across all trials (Fig. 5). We attribute this to differences in imagery production between those with low trial-level ratings of vividness compared to others (Fulford et al. 2018).

First, the parabolic pattern of accuracy during vivid dynamic imagery gives some insight into the multiple mechanisms affecting probe detection accuracy. In general, we proposed that priming involves the engagement of the visual pathway which enhances visual spatial perception. This has been shown before, whereby an intrinsic link between the primary visual areas and default mode network (DMN) has been established for the generation of

visual mental imagery (Zhang et al. 2018). The role of the DMN in mental imagery production has also been extensively theorized to describe the internalization of production of depictive vivid imagery (Xu et al. 2016; Lee et al. 2021).

In low-TSDVI participants we posit that vivid imagery generation is externalized and possibly gathered from non-visual sources (Dixon et al. 2014), while for high-TSDVI participants, vivid imagery is produced as a result of internalized processes involving the DMN and its coupling to the visual areas (Zhang et al. 2018). In the latter case, the ventral visual system is essentially primed, as possible mediator for subliminal detection. Importantly, this pattern negatively shifts during non-vivid imagery, highlighting the effect of vividness. Indeed we found that during non-vivid dynamic imagery, only the high-TSDVI group had inverted (degraded) accuracy (further discussed below), indicating that the priming effect in low-TSDVI individuals is unaffected by vividness (consistent with imagery which is less dependent on engaging the DMN), while in high-TSDVI individuals, it is indeed dependent on object vividness. Indeed, imagery priming has been correlated with the ability and neural correlates of externalizing or out-of-body projection of mental images (D'Angiulli et al. 2021; Azañón et al. 2025).

Neurobiologically, it has been reported that the generation of high-vividness items is less dependent on memory compared to low-vividness items, indicating that distinct neural mechanisms are required for the self-generated information (Lefebvre and D'Angiulli 2019b; Gjorgieva et al. 2022). This explains the pattern of the high-TSDVI group well, as it indicates that during vivid imagery, priming occurs likely as a result of DMN-visual area coupling, while during non-vivid imagery, distinct conceptual processes are required to produce low-vivid images, reduce the priming effect as DMN activity downregulates. The neural activations of low-vividness producing individuals also hints at some

explanation for an unchanging accuracy level in the low-TSDVI group. Low imaginers have been posited to draw on non-visual sources of knowledge when asked to visualize, while high imaginers may instead draw from internal visual sources, consistent with DMN-visual areas coupling (Zhang et al. 2018; D'Angiulli et al. 2021).

The fusiform gyrus, posterior cingulate, and parahippocampal gyri have been reproducibly shown as having activity that correlates with imagery vividness (Motoyama and Hishitani 2016; Fulford et al. 2018; Lee et al. 2022). Both fusiform gyrus and parahippocampal gyri are accordingly activated during subliminal detection (Meneguzzo et al. 2014; Dahlén et al. 2022), and so one explanation for enhanced subliminal detection is that imagery engages brain regions and prime activity for better detection of subliminal stimuli. It has also been noted that low-vividness individuals show greater activation of the inferior frontal gyrus, insula, cuneus, and anterior cingulate compared to high-vividness individuals, a pattern which has been attributed to a failure to suppress activity which interferes with vividness, or as a compensatory activation of regions with potential to drive the imagery process (Fulford et al. 2018).

The occurrence of 'inverse accuracy'

The repeated importance of vividness as a contributor of the accuracy-reversal effect, and further as a predictor of such an effect, suggest that it is the internal mental generation (as a function of vividness) which primes external spatial visual information amongst high-TSDVI individuals. We found that only those reporting high-TSDVI scores possess reduced detection (indeed a negative accuracy) in the subsequent control trials (Fig. 2). While paradoxical, we put forth a possible explanation for the accuracy reversal in which we argue interpretation as induced (albeit unconscious) identification of the probe where it was not. This discrepancy likely arises as a result of the task sequence, as task demands switch from mental imagery to control trials which did not demand imagery. As participants perform the mental imagery trial, they attempt to produce mental imagery projected at the screen in front of them, amongst high-TSDVI individuals, this is a faster process (see Fig. 1), replicating previous findings (Lefebvre and D'Angiulli 2019).

We identified that the subsequent unconscious detection of the probe stimulus is primed in participants during imagery, valid within the framework in which mental imagery engages regions which are dually tasked with processing subliminal incoming spatial information. Thus, even though the participant is not consciously aware of the stimulus probe, successful guesses tend to be at greater-than-chance level, as imagery engages the regions which process the incoming information (Motoyama and Hishitani 2016; Fulford et al. 2018; Lee et al. 2022).

In contrast, the control trials would require no generation of imagery, while continuing to attend to the screen (a process which similarly engages the same regions involved in vividness; Wyland et al. 2003). To achieve negative accuracy of a subliminal stimuli, we argue that some processing in the brain must still occur in order to know where the stimulus is not, and so our explanation posits the subsequent utility or differential processing of the incoming information. We argue that if brain centres processing these subliminal stimuli receive incoming information, but fail to process it given the lack of priming, then information of where becomes disjointed from information of what. We put forth that in this context the available information is captured in the conjecture that participants saw 'nothing, but somewhere'. We can apply this disjointed information to the dorsal and ventral visual

streams in which the dorsal stream (e.g. where/how) unconsciously processes the location (agnostic to the object; Almeida et al. 2010) while the ventral stream (e.g. what) fails to grasp the item itself (Mishkin et al. 1983).

The decision of where the object was must then resort to reverse inference, selecting the location where it could have been, as opposed to the place where 'nothing' was. This conjecture certainly requires further empirical support, as there is little work on the localization of subliminal items during forced-choice task demands; however, it serves as a possible explanation for how high-TSDVI individuals were able to achieve below-chance during non-imagery. The 'control condition effect' has been theorized in other studies, indeed Fulford et al. (2018) suggested that highvividness individuals undergo more involuntary imagery during subsequent control trials, leading to artefactual effects as a result. Any attempt to suppress this imagery in line with the control condition demands (i.e., none), might incidentally result in the effect we report here (as in artefactual reduction in 'imagery' fMRI activation in the vivid imagers when the control condition is subtracted from the imagery condition), although this account needs to be investigated further. Specifically, an important emerging link of these findings is the possible relationship between amodal completion of perceived objects and (possibly unconscious) spatial imagery (Nanay 2021). At the historical origin of the very idea of amodal completion, Benussi's investigations (sometimes using hypnotic manipulation) showed that the unconscious asensory persuasion or feeling of presence was a precursor of perceiving an object (Benussi and Musatti 2020). Decades later, the closely related concept of 'image search' was introduced within the context of perception-action cycle of organisms in ethology and neurobiology (Freeman 1983).

Conclusion

In all, our findings offer a novel explanation for the continued decline of the Perky effect (Dijkstra and Fleming 2023), indeed showing that in subliminal conditions, imagery can prime and enhance subliminal processing, particularly amongst individuals with low TSDVI or high TSDVI under vivid conditions. The effect of vividness is a crucial element in considering the processing of subliminal information, and the further contributions of individual levels of vivid imagery generating ability. We can also extend these explanations beyond theoretical interest, as employing subliminal stimuli during emotion exposure (Frumento et al. 2022), phobia exposure (Frumento et al. 2021), and other therapeutic interventions (Linehan and O'Toole 1982) can be augmented under the novel context of how vivid imagery can valence and prime the processing of subliminal visual information. Indeed age-related decline in mental imagery may soon be the target of interventive approaches in order to preserve what could be enhanced subliminal processing and perceptual ability (Craver-Lemley et al. 2010).

Author contributions

Gabriel Byczynski (Formal analysis [lead], Investigation [equal], Validation [equal], Visualization [lead], Writing—original draft [equal], Writing—review & editing [equal]) and Amedeo D'Angiulli (Conceptualization [lead], Data curation [equal], Funding acquisition [lead], Investigation [equal], Methodology [lead], Supervision [lead], Writing-original draft [equal], Writing-review & editing [equal]).

Conflict of interest

None declared.

Funding

None declared.

Data availability

Data used in this paper are available upon request to corresponding author.

References

- Alho J, Gotsopoulos A, Silvanto J. Where in the brain do internally generated and externally presented visual information interact? Brain Res 2023;1821:148582. https://doi.org/10.1016/j. brainres.2023.148582
- Almeida J, Mahon BZ, Caramazza A. The role of the dorsal visual processing stream in tool identification. Psychol Sci 2010;21:772-8. https://doi.org/10.1177/0956797610371343
- Azañón E, Pounder Z, Figueroa A et al. Individual variability in mental imagery vividness does not predict perceptual interference with imagery: a replication study of cui et al. (2007). J Exp Psychol Gen 2025;**154**:2043-57. https://doi.org/10.1037/xge0001756
- Bargh JA, Morsella E. The unconscious mind. Perspect Psychol Sci 2008;3:73-9. https://doi.org/10.1111/j.1745-6916.2008.00064.x
- Benussi V, Musatti CL. Psicologia sperimentale e teoria della forma: scritti 1922-1938. Mimesis, New York. 2020.
- Chang S, Lewis DE, Pearson J. The functional effects of color perception and color imagery. J Vis 2013;13:4-4. https://doi. org/10.1167/13.10.4
- Craver-Lemley C, Reeves A. Visual imagery selectively reduces 1987;**16**:599–614. https://doi. vernier acuity. Perception org/10.1068/p160599
- Craver-Lemley C, Reeves A. How visual imagery interferes with vision. Psychol Rev 1992;99:633-49. https://doi.org/10.1037/0033-
- Craver-Lemley C, Arterberry ME, Reeves A. Effects of imagery on vernier acuity under conditions of induced depth. J Exp Psychol Hum Percept Perform 1997;23:3-13.
- Craver-Lemley C, Bornstein RF, Alexander DN et al. Imagery interference diminishes in older adults: age-related differences in the magnitude of the Perky effect. Imagin Coan Pers 2010;29:307-22. https://doi.org/10.2190/IC.29.4.c
- Currie G. Visual imagery as the simulation of vision. Mind Lang 1995; 10:25-44. https://doi.org/10.1111/j.1468-0017.1995.tb00004.
- Dahlén AD, Schofield A, Schiöth HB et al. Subliminal emotional faces elicit predominantly right-lateralized amygdala activation: a systematic meta-analysis of fMRI studies. Front Neurosci 2022;16:868366. https://doi.org/10.3389/fnins.2022.868366
- D'Angiulli A, Kenney D, Pham DAT et al. Neurofunctional symmetries and asymmetries during voluntary out-of- and withinbody vivid imagery concurrent with orienting attention and visuospatial detection. Symmetry 2021;13:1549. https://www.mdpi. com/2073-8994/13/8/1549. https://doi.org/10.3390/sym13081549
- D'Angiulli A, Laarakker C, Buchanan DM. An ART tour de force on mental imagery: vividness, individual bias differences, and complementary visual processing streams. Information 2024;15:59. https://www.mdpi.com/2078-2489/15/1/59. https:// doi.org/10.3390/info15010059

- D'Angiulli A, Reeves A. The relationship between self-reported vividness and latency during mental size scaling of everyday items: phenomenological evidence of different types of imagery. Am J Psychol 2007;120:521-51. https://doi.org/10.2307/20445424
- D'Angiulli A, Roy R. The frog-manikin holding the blue parasol umbrella: imaginative generativity in evolution, life, and consciousness. Curr Opin Behav Sci 2024;58:101397. https://doi. org/10.1016/j.cobeha.2024.101397
- D'Angiulli A, Runge M, Faulkner A et al. Vividness of visual imagery and incidental recall of verbal cues, when phenomenological availability reflects long-term memory accessibility [original research]. Front Psychol 2013;4:1-18. https://doi.org/10.3389/ fpsyg.2013.00001
- Dijkstra N, Fleming SM. Subjective signal strength distinguishes reality from imagination. Nat Commun 2023;14:1627. https://doi. org/10.1038/s41467-023-37322-1
- Dijkstra N, Bosch SE, van Gerven MAJ. Vividness of visual imagery depends on the neural overlap with perception in visual areas. J Neurosci 2017;37:1367-73. https://doi.org/10.1523/ jneurosci.3022-16.2016
- Dixon ML, Fox KCR, Christoff K. A framework for understanding the relationship between externally and internally directed cognition. Neuropsychologia 2014;62:321-30. https://doi.org/10.1016/j. neuropsychologia.2014.05.024
- Farah MJ. The neural basis of mental imagery. Trends Neurosci 1989;12:395-9. https://doi.org/10.1016/0166-2236(89)90079-9
- Freeman WJ. The physiological basis of mental images. Biol Psychiatry 1983:**18**:1107-25.
- Frumento S, Menicucci D, Hitchcott PK et al. Systematic review of studies on subliminal exposure to phobic stimuli: integrating therapeutic models for specific phobias [systematic review]. Front Neurosci 2021;15:1–18. https://doi.org/10.3389/fnins.2021.654170
- Frumento S, Gemignani A, Menicucci D. Perceptually visible but emotionally subliminal stimuli to improve exposure therapies. Brain Sci 2022; 12:867. https://doi.org/10.3390/brainsci12070867
- Fulford J, Milton F, Salas D et al. The neural correlates of visual imagery vividness - an fMRI study and literature review. Cortex 2018;105:26-40. https://doi.org/10.1016/j.cortex.2017.09.014
- van Gaal S, Lamme VAF. Unconscious high-level information processing: implication for neurobiological theories of consciousness. Neuroscientist 2012;18:287-301. https://doi.org/10.1177/ 1073858411404079
- Gjorgieva E, Geib BR, Cabeza R et al. The influence of imagery vividness and internally-directed attention on the neural mechanisms underlying the encoding of visual mental images into episodic memory. Cereb Cortex 2022;33:3207-20. https://doi.org/10.1093/ cercor/bhac270
- Grossberg, S. (2021). Conscious Mind, Resonant Brain: How each Brain Makes a Mind. Oxford University Press, New York. https://doi. org/10.1093/oso/9780190070557.001.0001.
- John OP, Donahue EM, Kentle RL. Big five inventory. J Pers Soc Psychol 1991;**60**:348–61.
- Kosslyn SM, Brunn J, Cave KR et al. Individual differences in mental imagery ability: a computational analysis. Cognition 1984;18: 195-243. https://doi.org/10.1016/0010-0277(84)90025-8
- Lee S, Parthasarathi T, Kable JW. The ventral and dorsal default mode networks are dissociably modulated by the vividness and valence of imagined events. J Neurosci 2021;41:5243-50. https:// doi.org/10.1523/jneurosci.1273-20.2021
- Lee S, Parthasarathi T, Cooper N et al. A neural signature of the vividness of prospective thought is modulated by temporal proximity during intertemporal decision making. Proc Natl Acad Sci 2022;**119**:e2214072119. https://doi.org/10.1073/pnas.2214072119

- Lefebvre E, D'Angiulli A. Imagery-mediated verbal learning depends on vividness-familiarity interactions: the possible role of dualistic resting state network activity interference. Brain Sci 2019a;9:143. https://www.mdpi.com/2076-3425/9/6/143. https:// doi.org/10.3390/brainsci9060143
- Lefebvre E, D'Angiulli A. Imagery-mediated verbal learning depends on vividness-familiarity interactions: the possible role of dualistic resting state network activity interference. Brain Sci 2019b;9:143. https://doi.org/10.3390/brainsci9060143
- Linehan E, O'Toole J. Effect of subliminal stimulation of symbiotic fantasies on college student self-disclosure in group counseling. J Couns Psychol 1982;29:151-7. https://doi. org/10.1037/0022-0167.29.2.151
- Marks DF. Visual imagery differences and eye movements in the recall of pictures. Percept Psychophys 1973a;14:407-12. https://doi. org/10.3758/BF03211175
- Marks DF. Visual imagery differences in the recall of pictures. Br J Psychol 1973b;64:17-24. https://doi.org/10.1111/j.2044-8295.1973. tb01322.x
- Marks DF. I am conscious, therefore, I am: imagery, affect, action, and a general theory of behavior. Brain Sci 2019;9:107https:// www.mdpi.com/2076-3425/9/5/107. https://doi.org/10.3390/ brainsci9050107
- Meneguzzo P, Tsakiris M, Schioth HB et al. Subliminal versus supraliminal stimuli activate neural responses in anterior cingulate cortex, fusiform gyrus and insula: a meta-analysis of fMRI studies. BMC Psychology 2014;2:52. https://doi.org/10.1186/ s40359-014-0052-1
- Mishkin M, Ungerleider LG, Macko KA. Object vision and spatial vision: two cortical pathways. Trends Neurosci 1983;6:414-7. https://doi.org/10.1016/0166-2236(83)90190-X
- Motoyama H, Hishitani S. The brain mechanism that reduces the vividness of negative imagery. Conscious Cogn 2016;39:59-69. https://doi.org/10.1016/j.concog.2015.11.006
- Nanay B. Unconscious mental imagery. Philos Trans R Soc B: Biol Sci 2021;376:20190689. https://doi.org/10.1098/rstb.2019.
- Pearson J. The human imagination: the cognitive neuroscience of visual mental imagery. Nat Rev Neurosci 2019;20:624-34. https:// doi.org/10.1038/s41583-019-0202-9
- Pearson J, Clifford CWG, Tong F. The functional impact of mental imagery on conscious perception. Curr Biol 2008;18:982-6. https:// doi.org/10.1016/j.cub.2008.05.048
- Pearson J, Rademaker RL, Tong F. Evaluating the Mind's eye: the metacognition of visual imagery. Psychol Sci 2011;22:1535-42. https://doi.org/10.1177/0956797611417134
- Perky CW. An experimental study of imagination. Am J Psychol 1910;21:422-52. https://doi.org/10.2307/1413350

- Reeder RR. Individual differences shape the content of visual representations. Vis Res 2017;141:266-81. https://doi.org/10.1016/j. visres.2016.08.008
- Reeves A, Segal SJ. Effects of visual imagery on visual sensitivity and pupil diameter. Percept Mot Skills 1973;36:1091-8. https://doi. org/10.2466/pms.1973.36.3c.1091
- Reeves A, Grayhem R, Craver-Lemley C. The Perky effect revisited: imagery hinders perception at high levels, but aids it at low. Vis Res 2020;**167**:8–14. https://doi.org/10.1016/j.visres.2019.12.004
- Runge M, Bakhilau V, Omer F et al. Trial-by-trial vividness self-reports versus VVIQ: a meta-analytic comparison of behavioral, cognitive and neurological correlations. Imagin Cogn Pers 2015;35:137-65. https://doi.org/10.1177/0276236615587490
- Runge MS, Cheung MW-L, D'Angiulli A. Meta-analytic comparison of trial- versus questionnaire-based vividness reportability across behavioral, cognitive and neural measurements of imagery. Neurosci Conscious 2017;**2017**:1–13. https://doi.org/10.1093/nc/nix006
- Sandberg K, Del Pin SH, Overgaard M et al. A window of subliminal perception. Behav Brain Res 2022;426:113842. https://doi. org/10.1016/j.bbr.2022.113842
- Segal SJ, Fusella V. Influence of imaged pictures and sounds on detection of visual and auditory signals. J Exp Psychol 1970;83: 458–64. https://doi.org/10.1037/h0028840
- Segal SJ, Gordon P-E. The Perky effect revisited: blocking of visual signals by imagery. Percept Mot Skills 1969;28:791-7. https://doi. org/10.2466/pms.1969.28.3.791
- Su J, Van Boxtel JJ, Lu H. Social interactions receive priority to conscious perception. PLoS One 2016;11:e0160468. https://doi. org/10.1371/journal.pone.0160468
- Syed AA, Neelofur S, Moran A et al. Exploring the vividness of mental imagery and eidetic imagery in people with intellectual disability (ID) in comparison with typically developing (TD) individuals. Heliyon 2020;6:e05429. https://doi.org/10.1016/j.heliyon.2020. e05429
- Westwood, D. A. (2009). Visual pathways for perception and action. In M. D. Binder, N. Hirokawa, & U. Windhorst (Eds.), Encyclopedia of Neuroscience (pp. 4324-7). Berlin Heidelberg: Springer. https://doi. org/10.1007/978-3-540-29678-2_6362
- Wyland CL, Kelley WM, Macrae CN et al. Neural correlates of thought suppression. Neuropsychologia 2003;41:1863-7. https:// doi.org/10.1016/j.neuropsychologia.2003.08.001
- Xu X, Yuan H, Lei X. Activation and connectivity within the default mode network contribute independently to future-oriented thought. Sci Rep 2016;**6**:21001. https://doi.org/10.1038/srep21001
- Zhang Z, Zhang D, Wang Z et al. Intrinsic neural linkage between primary visual area and default mode network in human brain: evidence from visual mental imagery. Neuroscience 2018;379: 13-21. https://doi.org/10.1016/j.neuroscience.2018.02.033