



Review

Progress in cognitive neuroscientific studies of visual awareness

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Abstract

The psychological and neural mechanisms of consciousness are among the most baffling problems in cognitive neuroscience. In this field, visual awareness is a topic that has been largely investigated, due to easy manipulation and measurable effects. The present article begins with the phenomena of dissociations between visual awareness and visual stimulus, visual awareness and visual attention, as well as visual awareness and vision-guided behavior, along with the corresponding experimental evidence. Furthermore, the neural mechanism of visual awareness is also discussed. It has been generally believed that visual awareness is the function of higher-order cerebral areas; however, recent discoveries have demonstrated that feedback from higher- to lower-order cortex areas is necessary for generating consciousness. The present article presents an in-depth analysis regarding this feedback process, and exploring its relationship with the generation and mechanisms of consciousness. Finally, theoretical controversies and discrepancies, as well as result conflicts from various studies, have been collected, compared and discussed. Because the field of consciousness continues to be an extremely mysterious and complicated psychological phenomenon, there is a great need for further studies to explore and clarify this topic.

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1. Introduction

What is consciousness? This question has been discussed by philosophers and psychologists since ancient times. Nevertheless, centuries of research have failed to provide a widely accepted definition of consciousness [1]. Most researchers do agree, however, that consciousness is a collection of an organism's subjective experiences of objects in the surrounding world, as well as of internal psychological and biological activities [2]; these experiences are the outcome of neural activities within the brain. Although many theories have proposed that phenomenal consciousness emerges from complicated neural activities,

the mechanisms involved remain unclear. Visual awareness, which is generally defined as the subjective visual experience, is one of the most researched areas in the field of consciousness, parallel with auditory awareness, tactical awareness, etc. Before exploring and discussing consciousness in a general sense, visual awareness, which can be conveniently operationalized, serves as a good starting point. However, many years of dedicated research on conscious vision have failed to answer the question as to what consciousness really is. In contrast, the research has rather told us what consciousness is NOT. Through these studies, researchers have attempted to unveil the nature of consciousness. Many recent studies on visual awareness have endeavored to reveal dissociations between visual awareness and other factors, such as visual stimuli, visual attention, and vision-guided behavior, which will be reviewed in the next section.

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2. Dissociations in the field of visual awareness

2.1. Dissociation between visual awareness and visual stimuli

The dissociation between visual awareness and visual stimuli can be understood in two ways. On the one hand, a human being does not establish a detailed representation of the world he is looking at like a camera does. In contrast, not all information that reaches the retina can attain consciousness. The discovery of many visual blindness phenomena, such as change blindness [3,4], motion-induced blindness [5,6], and inattention blindness [7–9], has lent support to this seemingly astonishing theory. Under certain conditions, a normal observer can fail to perceive a salient visual stimulus (or its change), although it is usually perceivable. Change blindness refers to the failure to detect changes between two successively presented scenes; motion-induced blindness is the sporadic disappearance and reappearance of a salient target stimulus presented against a moving background; inattention blindness refers to when an observer dedicates his/her attention to a demanding main task and fails to detect the appearance of an outstanding, yet unexpected, stimulus presented in the visual field. Mack and Rock [10] determined that as many as 25% of their subjects failed to observe an unexpected, salient, peripheral stimulus. When this stimulus appeared in the fovea, the percentage surged to 80%. In a more dramatic experiment conducted by Simons and Chabris [7], subjects that were busy counting basketball passes even failed to see a gorilla walking right through the display. These studies together confirm the fact that visual stimuli do not necessarily lead to corresponding subjective experience, namely, visual awareness.

On the other hand, the generation of visual awareness does not always rely on external visual input. Common-place phenomena, such as imagination and dreams, as well as phosphenes induced by TMS (as will be mentioned later in this review), are all cases where subjective visual experience exists, while external visual information input does not. Visual awareness is a broad concept encompassing various subjective visual experiences. It can refer to awareness of external visual stimuli, as well as visual representation internally generated (e.g., mental images).

2.2. Dissociation between visual awareness and visual attention

Visual awareness and visual attention have always been closely related – so close, in fact, that they are often considered synonymous. The various forms of visual blindness mentioned above also suggest that attention plays an important role in detection and visual awareness. Some researchers even went a step further to claim that there is no consciousness without attention [11]. However, the relationship between consciousness and attention might be more complex than that. As mentioned above, empirical evidence has indicated that the generation of visual aware-

ness is dependent on visual attention [12]. However, emerging evidence leads to the conclusion that consciousness and attention might be two distinct processes after all [13,14]. Again, we take the example of inattention blindness. As its name implies, the failure of unexpected stimulus to enter consciousness seems to be due to lack of attention; however, many studies do not support this notion. A very recent study [15] has shown in an inattention blindness experiment that main task performance suffers impairment if, and only if, the subject is unaware of the unexpected stimulus. In the meantime, observers that claimed they did not see the unexpected stimulus gave a higher-than-chance performance when facing a forced-choice of stimulus properties, such as shape. This result indicates that even when not perceived, unexpected stimulus still occupies a portion of the subjects' attentional resources and receives processing to a certain degree. Experiments on motion-induced blindness also suggest a distinction between attention and consciousness. In a typical experiment, where a high-contrast stationary target was presented on a continuously moving background of relatively lower contrast, the target repeatedly disappears and reappears in the observer's percept. Studies have demonstrated that targets that are more salient (therefore require more attention), result in a greater possibility and longer duration of disappearance [5,6]. Furthermore, Jiang et al. [16] employed the Continuous Flash Suppression (CFS) [17] paradigm, and found that erotic pictures affect the allocation of spatial attention, even when they are not consciously perceived.

Lamme [14] explained the dissociation between consciousness and attention from a unique angle, by dividing consciousness into two subcategories, namely, transient consciousness and reportable consciousness, which are similar to Block's "phenomenal consciousness" and "access consciousness" [18]. Lamme used change blindness as an example and postulated that even in the complicated scenario of a change blindness experiment, subjects were still able to perceive most information; however, information was overwritten by the successor before it was transformed to reportable consciousness. If the subjects were cued as to where the change should occur prior to appearance of the post-change picture, they performed almost 100% accurately. Similar explanations have been proposed for inattention blindness, which is why some researchers prefer to call it inattention amnesia [19].

2.3. Dissociation between visual awareness and vision-guided behavior

Another typical dissociation is the one between visual awareness and vision-guided behavior, which, compared with the distinction between attention and consciousness, is easier to understand, because many of our daily activities rely heavily on visual processing and can be performed without conscious effort. A common example is that a driver can arrive safely at his destination while thinking about other things, not aware of how he has been driving. Stricter

scientific evidence is available from various studies on subliminal processing and blindsight. Milner and Goodale have performed many studies on this subject. For example, patient D.F., who had suffered bilateral lesion in his ventral pathway and was therefore unable to identify the size and orientation of an object, was able to accurately navigate his grasping movements [20]. As early as 1992, Goodale et al. [21–23] proposed the theory of two distinct visual pathways responsible for two types of vision. The ventral pathway, according to this theory, is responsible for object identification, otherwise termed “vision for perception”, while the dorsal pathway coordinates and supervises body movements, termed “vision for action”. In a very recent paper [24], Milner and Goodale further clarified that the term “perception” in their dichotomy refers to consciousness, and includes preconscious and unconscious representations that can transfer to consciousness under certain conditions. The term “perception” is, more or less, the equivalent of Lamme’s “transient consciousness”, or Wolfe’s “phenomenal consciousness”.

3. Neural mechanisms of visual awareness

It is not enough to merely distinguish consciousness from other psychological processes on a functional level. Studies have endeavored to separate them according to the underlying neural mechanisms to answer, “what is consciousness?” on a neural level. The discovery of feedback processing has undoubtedly provided valuable clues.

3.1. Traditional opinion

The traditional model of visual awareness is a hierarchy model [25], which suggests that brain processes visual information in a hierarchical way. Visual information flows from lower visual cortexes to higher ones in a fast feedforward sweep (FFS), receiving more complex and detailed processing at each level [26]. Some studies have hypothesized that only higher extra-striate cortexes are directly involved in awareness; a lesion to V1 produces a blind field only because it blocks information input. Crick and Koch originally proposed that only a cortical area directly connected to the frontal lobe could contribute to consciousness. Because V1 lacks a direct connection to the frontal lobe, they stated that we are not “aware of neural activity in primary visual cortex” [27]. This hierarchical model takes into consideration only the forward flow of information, and ignores the possible role of feedback processes from higher-level cortexes to lower-level ones. According to the hierarchical model, V1 serves as an information relay, which means that once information has passed through it, V1 is not involved in later processes or the generation of visual awareness.

3.2. Recent progress: the role of feedback processing

Immediately following the hierarchical model is the prediction that suppressing or disrupting neural activities in

V1 will not affect visual awareness once information has passed through V1. However, many recent experimental results contradict this corollary. Increasingly, studies have demonstrated direct or indirect evidence that feedback processes from higher visual cortexes to V1 are crucial for visual awareness.

Electrophysiological studies have illustrated that in the monkey vision system, many feedback connections, other than feedforward ones, exist [28]. Because animals are incapable of subjective reports, these experiments provide little help in understanding the relationship between feedback processing and consciousness, which exemplifies the need for human-subject studies in this field. In studies employing human subjects, the most commonly used technology is transcranial magnetic stimulation (TMS). It has been shown that TMS, applied to a certain cortical area, can disrupt its activities. When TMS strength is above a certain threshold, it can induce stationary phosphenes in V1 and moving phosphenes in the V5 [29,30].

In a lesion study, Cowey and Walsh [29] applied TMS to V5 to produce moving phosphenes. Because phosphene awareness does not rely on external visual input, they studied the role of feedback projecting from the V5 to V1 to elicit visual awareness by comparing the V5 TMS effects on a blind subject (P.S., whose visual nerves were severed, but whose V1 was intact), a brain lesion subject (G.Y., whose left striate area was completely destroyed), and normal subjects. Cowey and Walsh found that normal subjects were aware of phosphenes; the blind subject, P.S., whose V1 was intact, could also perceive phosphenes, but the lesion patient, G.Y., could perceive phosphenes only when TMS was applied to his right V5. Moreover, TMS delivered to the V5 ipsilateral to his V1 lesion failed to elicit a response. The phosphenes in this experiment were produced by TMS applied to the V5, instead of real visual input; therefore, according to the hierarchical model, because visual information already reached the higher V5, V1 should not be involved with visual awareness. Results from this experiment illustrate that for visual experience produced directly in higher visual cortexes, V1 still plays an important role. Such a finding suggests that signals from higher cortical areas to lower ones, namely, the feedback process, are crucial for the generation of visual awareness.

Lesion studies have intrinsic disadvantages. Firstly, lesion patients are rare. Secondly, the location and extension of lesions cannot be controlled. Therefore, researchers in the above study could not be sure whether the failure to perceive phosphenes was due to V1 lesion or other factors, such as operational errors in TMS experimentation, inaccurate allocation of TMS, or individual subject differences (not all normal subjects can perceive phosphenes [31]). Pascual-Leone and Walsh [31] expanded this experiment to normal subjects by stimulating both V1 and V5 with two TMS coils.

In their experiment, Pascual-Leone and Walsh applied two single pulse TMS, respectively, to V1 and V5.

The magnetic stimulation to the V5 was strong enough to produce moving phosphenes, while sub-threshold V1 stimulation, serving only to suppress V1 activities, was applied at different time intervals. By systematically manipulating the V5–V1 stimulus onset asynchrony (SOAs), they intended to capture backprojections from the V5 to V1 to investigate the role of feedback processes in visual awareness. Subjects were asked to rate their awareness of phosphenes on a 4-point forced-choice scale (Fig. 1). Since moving phosphenes were directly elicited by the V5 TMS, no feedforward process was involved. If, at a certain moment, V1 disruption led to impaired awareness of moving phosphene, it can be inferred that visual information flows backward from the V5 to V1 and this backprojection is necessary for visual awareness. This study showed that V1 TMS applied at 5–45 ms after onset of V5 TMS resulted in impaired awareness of phosphenes, and the greatest impairment appeared around 25 ms V5–V1 TMS SOA. This experiment not only extended the conclusion of lesion studies to normal subjects, further confirming the causal relationship between feedback process and visual awareness, but also showed that backprojection was very fast.

Following this direction, some studies have further generalized results from internally elicited phosphenes to real visual inputs. Silvanto et al. [32] presented subjects with moving dots and applied double pulse TMS (dTMS) to V1 and V5 at various delays. They found that after onset of external visual stimuli, V1 dTMS at 40–60 ms (experiment 3), V5 dTMS at 60–80 ms (experiment 1), or V1 dTMS at 80–100 ms (experiment 1) produced impairment in motion detection performance. The three time windows indicated the pathway of visual information flow: from the lower visual areas to the higher visual areas, and then back to the lower visual areas.

Among human-subject experiments, evidence supporting the importance of feedback processing was also

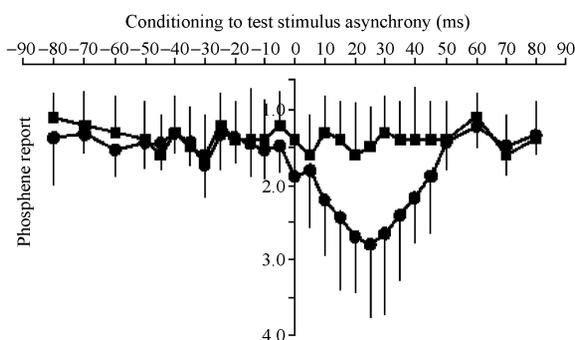


Fig. 1. Results from Pascual-Leone and Walsh's experiment (adapted from Ref. [31]). The horizontal axis represents V5–V1 TMS SOAs: negative values indicate that V1 received TMS prior to V5, and positive values indicate that V1 was stimulated after V5. The vertical axis represents levels of awareness: phosphene elicited by V5 TMS was (1.0) present and moving; (2.0) present, but not sure whether it was moving or not moving differently; (3.0) present, but stationary; (4.0) no phosphene was observed.

obtained in tasks other than the visual motion task. Overgaard et al. [33] applied TMS to V1 of normal subjects to investigate the feedback process in a variety of visual tasks. In their experiment, the subject was asked to report three properties (location, shape, and color) of a briefly presented (192 ms) target, and to provide a confidence rating. Results demonstrated that although the percentage of correct reports remained unaffected by V1 TMS at different intervals after visual stimuli, subject confidence was significantly decreased at the 120-ms interval. The authors proposed that these results were in favor of the feedback theory; in other words, TMS to V1 disrupted the normal feedback process and thereby decreased the subject's level of consciousness (reflected in reduced confidence). According to the authors, the fact that feedforward process was less affected by V1 TMS in this experiment might indicate that the feedforward process does not rely entirely on ventral processing, while the ventral pathway is more important for feedback processing.

The TMS technique provides great advantages to explore neural processes underlying consciousness, such as reversibility of suppression and fine temporal resolution. Other techniques, such as functional magnetic resonance imaging (fMRI) and event-related potential (ERP), have also produced valuable results. For example, Pins and ffytche [34] discovered that an early positive component (P1) is related to consciousness. Other studies demonstrated that a posterior negativity at about 200 ms, which they termed "visual awareness negativity" (VAN), correlated with whether a stimulus had entered consciousness [35,36]. Some fMRI studies also found that the visual pathway from V1 to inferior-temporal lobe was related to consciousness [37–39]. However, due to ERP's low spatial resolution and fMRI's low temporal resolution, these two techniques were not often used to analyze the feedback process. Nevertheless, several recent studies deserve mention. Sterzer et al. [40] utilized fMRI to examine activities in cortical areas corresponding to the path of apparent motion (AM). They generated a curved AM path (see Fig. 2a), so that the actual stimuli (two, tilted, flashing bars) and the AM path (as indicated by a double-ended, grey arrow) fell in different quadrants, making it convenient to analyze the corresponding V1 areas separately. The results showed that, compared to the empty quadrant, the quadrant traversed by the AM path (indicated by the small circle in Fig. 2a) produced higher activation, which confirmed previous results. In addition, Sterzer et al. employed a new method – Dynamic Causal Modeling (DCM) [41] – to analyze data and compare two possible models (Fig. 2b). The two models they proposed have two different hypotheses: Model I assumed that V5 feedback contributed to V1 activation, while Model II additionally included contributions from intrinsic, lateral connections within V1. The data analysis results favored the first model, which emphasized feedback contribution.

A recent study using high-density ERP also lends support to connection between feedback process and visual

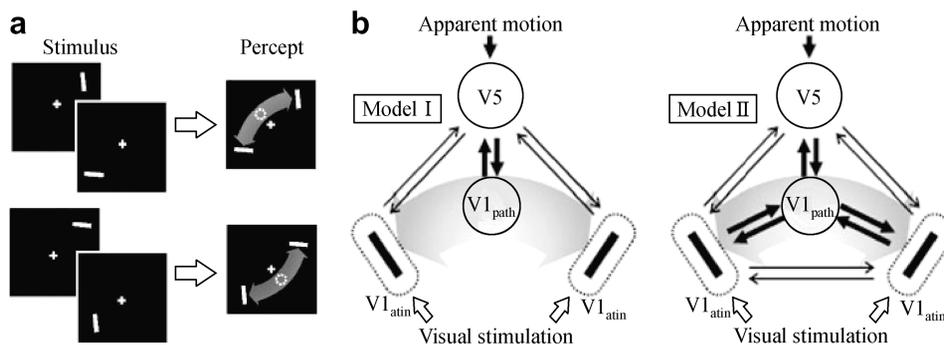


Fig. 2. Visual stimuli and models in Sterzer et al.'s experiment (adapted from Ref. [40]). (a) AM path; (b) comparing two models using DCM.

awareness [42]. In a common-onset visual masking (COVM) paradigm, occipital P2 appeared at around 220 ms, and the amplitude correlated with the awareness level. It was suggested that this late component reflected reactivation of the lower-level cortex, which related to feedback process, as proposed by Enns et al. [43].

Together, these studies confirmed the existence and importance of feedback processing in visual awareness in various ways. They typically investigated the role of feedback processing by capturing related late neural activities in lower visual areas. Although minor discrepancies exist in terms of a specific time course, the general ideas and results remain similar.

3.3. Theoretical model

Hochstein and Ahissar [44] proposed that feedforward and feedback processes are functionally different. Feedforward processes are automatic and implicit, and consciousness, which emerged at the top of cortical hierarchy, is abstract and categorical (“forest before trees”). To parse vision in a more detailed way, the brain needs feedback processes to focus on certain lower-level units to integrate information from both high- and low-levels.

Lamme [2,45,46] also suggested that feedforward and feedback in vision processing are two distinct processes (Fig. 3). In a fast-forward sweep, information is processed in a hierarchical manner: lower levels are responsible for lower levels of processing, and with each step, information reaches a higher stage, thereby receiving higher processing. As soon as information reaches a cortical area, interactions between this region, and lower regions that were previously

activated, immediately begin to be implemented by parallel, feedforward, and feedback connections. Lamme postulated that when information reaches higher areas in temporal, parietal, or even the frontal lobes, phenomenal consciousness does not necessarily follow. Recurrent processing between higher areas and lower areas, in particular, between extra-striate areas and V1, is the necessary prerequisite for vision to enter access consciousness.

Lamme's theory is closely related to the two classical visual pathways: the dorsal pathway and the ventral pathway. The dorsal pathway goes from V1 to V5/MT, followed by the parietal areas primarily involved in visual stimulus for locationing and motion processing. The ventral pathway includes V1, V2, VP, V4, and inferior-temporal gyrus, which are involved in object recognition. Goodale et al. [21–24,47] distinguished two forms of vision corresponding to the two pathways as “vision for action” and “vision for perception”, respectively. Animal experiments have demonstrated that V1 lesions affect the dorsal pathway much less than the ventral pathway [28]. Goodale et al.'s studies with human subjects illustrated interesting dissociations between the two pathways: perception could be distorted by context, through which illusions were created, such as the Ebbinghaus–Titchener illusion. However, when subjects were attempting to grasp an object, the aperture between their fingers was not affected by context at all, correlating only with the actual size of the object. It was suggested that illusions are developed in the perception-related ventral pathway, associated directly with consciousness, while the dorsal pathway, which is responsible for coordinating body movements and accurate positioning, is considered to be unconscious.

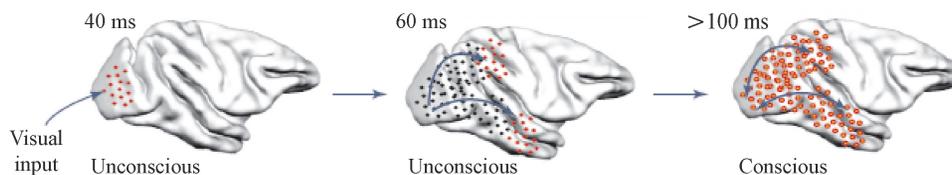


Fig. 3. Lamme's schematic of feedforward-feedback time course (adapted from Ref. [46]). Lamme believed that feedforward process is related to action, while feedback process is related to consciousness. Visual information reaches the brain 40 ms after stimulus onset, and thereafter travels rapidly to the extra-striate cortex. After 100 ms, feedforward processes continue to guide action, while feedback processes transfer information back to lower areas, such as V1.

Lamme agreed with this hypothesis and believed that feedback processes in the ventral pathway bear more relevance to visual awareness.

A large number of studies fit well in this hypothesis; however, some outliers still remain. For example, in a forced-choice paradigm, a blindsight patient made above-chance judgment, not only about properties processed by the dorsal pathway, but also properties thought to be more relevant to the ventral pathway, such as color [48] and facial expressions [49].

3.4. Analysis and comparison of relevant experiments

Although the existence and importance of feedback processing is receiving support from a growing number of studies, there are still many discrepancies between the various results and methods. The first dilemma is the lack of a proper definition for consciousness. Because a commonly acknowledged definition has not been decided upon, the various experiments have used different tasks and criteria, according to the author's own understanding. Some studies involved subjective report, or detection task, which required the subjects to report their state of awareness, including whether or not they were aware of the stimulus and their confidence level. Others adopted stricter standards, such as forced-choice of motion direction [50]. Contrasting definitions and tasks have yielded results that are conflicting and confusing. As mentioned earlier, vision awareness and visual guided behavior are two distinct processes. Therefore, patients suffering from a V1 lesion could perform better than chance when they were required to guess the properties they "did not see" [51]. However, despite this fact, some experiments still used the forced-choice task to assess consciousness. Take Becker and Zeki's experiment [50] as an example, they used forced-choice of direction as a criterion for consciousness: if performance was not better than chance, then the subject was not aware of the stimulus. If the performance was significantly better than chance, then the subject was aware of it. Others have used subjective reports to determine the border between consciousness and unconsciousness, discovering dissociations between forced-choice performance and level of awareness [52]. In Overg-

aard et al.'s study [33], however, forced-choice and confidence did not dissociate when the property involved was color or shape; however, in terms of location, forced-choice performance remained above-chance, despite confidence variations. These conflicts are probably a result of different ways of operationalizing consciousness.

A second discrepancy is the time needed for information to return from higher areas (e.g., V5) to lower areas (e.g., V1), ranging from 20 ms [31] to as long as 200–240 ms [53]. Various factors could be responsible for this discrepancy, such as stimulus type, task, and TMS intensity [54]. Some researchers have even proposed that different components of feedback were captured in different experiments [53]. By applying repeated TMS to V1, Juan and Walsh discovered [53] that in conjunction detection task (which compared to the feature detection task has a greater signal-noise ration), V1 was involved during the first 100 ms (from stimulus onset); V1 involvement was also detected as late as 200–240 ms. It was proposed that V1 activities during the first 100 ms indicated recurrent transmissions within V1, while the late component implicated that V1 might have more than one role in feedback processing. It is possible that this late component reveals reregistering of the higher areas of information through V1 reception field. It might even be possible that only the late component is consciousness-related. Table 1 is a collection and comparison of relevant experiments involving visual motion processing.

The third dilemma is that there is very little knowledge on how this feedback process produces consciousness and what the exact role of V1 in the generation of consciousness is, although ample evidence now exists to prove the existence and importance of feedback processing. Several theories have been proposed: Lamme [14] suggested that feedback takes effect in binding, while Hupe et al. [56] proposed that feedback processing serves to focus and amplify activities in the lower areas. Similarly, Hochstein and Ahissar [44] postulated that although consciousness begins at the top level of hierarchy, it needs to focus on specific neurons in V1. The role of V1 in feedback processing is likened to an "active blackboard" [57], or a "look-up table" [53]. Because V1 neurons have very small receptive fields, V1

Table 1
Comparison of TMS studies on feedback processing.

Studies	Visual stimuli	Visual stimuli duration	Task	Time of largest impairment	
				V1	V5
Pascual-Leone and Walsh [31]	None (phosphenes)	–	Motion detection, subjective report	~25 ms ^③	–
Beckers and Hoemberg [55]	Moving dots (2.2°/s ^①)	140 ms	Motion direction judgment, forced-choice	70–80 ms	0 ms
Beckers and Zeki [50]	Moving dots (11°/s ^①)	28 ms	Motion direction judgment, forced-choice + confidence	~70 ms	0 ms
Silvanto et al. [32]	Random moving dots (1.7°/s ^②)	48/64 ms (adjusted according to each subject)	Motion detection, subjective report	80–100 ms ^④	60–80 ms ^④

Note: Some speeds in this table were provided directly by the experimenters (marked by ①); others were transformed (marked by ②). Pascual-Leone and Walsh's experiment did not use any external visual stimulus, time zero is the onset of V5 TMS (marked by ③); in Silvanto et al.'s experiment, time was calculated relative to stimulus offset (marked by ④); the other experiments were all relative to stimulus onset.

should not be aware of the big picture; higher-level neurons have larger receptive fields, which can provide them with the “main idea”; however, they have inevitably lost some spatial information. Therefore, recurrent information processing between higher-level cortices and V1 is viewed by some to be a “hypothesis testing” process; namely, feedforward sweep may activate several possible representations, and feedback process chooses the most likely one. Di Lollo et al. [58], who suggested that feedback processing can be used to explain common-onset masking, explained why visual representations produced by feedforward processes must be reconfirmed through feedback: (1) feedforward processes can generate more than one representation, and feedback can eliminate ambiguity; (2) feedforward processes lose spatial accuracy, and feedback processes can recompense it. In addition, some studies disagree with the indispensability of V1 in consciousness. For example, Zeki et al. [59] demonstrated that a patient suffering from a V1 lesion could not distinguish high-speed motion directions in his blind field; however, he claimed to “see” the motion, although this form of “seeing” was somewhat different from normal visual awareness. Moreover, some experimental details are worth noting [31]. For example, when Pascual-Leone and Walsh chose the site of V1 TMS, they ensured that stationary phosphenes invoked in V1 covered the exact area of moving phosphenes induced by V5 TMS. This seems to imply the following assumption: in feedback processes, V1 still functions according to each neuron’s own receptive field, rather than working as a whole or in other ways. If this were true, then the “look-up table” analogue would be pretty close. Indirect support for this postulation comes from Sterzer et al.’s study [40], which determined V1 areas that corresponded to the AM path were more active. Nevertheless, when pooled across the entire V1, the area exhibited no significant activation. This result seems to indicate that feedback signal is confined to the AM path, rather than diffusing through the entire V1. However, anatomical studies contradict this hypothesis; some studies have shown that feedforward connections are “like-with-like”. For example, all “nodes” from the path from layer 4B of V1 to the thick stripes of V2, and then to V5, are related to motion. However, feedback connections are different; feedback connections from higher areas to lower areas occur in a diffused manner. For example, the feedback pathway from V5 to V2 does not confine itself to thick stripes; rather, it includes thin stripes and interstripes. However, as Juan and Walsh [53] proposed, another possibility must be considered: these studies all captured the early component of feedback processing, and the late component may facilitate the generation of consciousness in a different way.

Finally, most TMS experiments rely on anatomical landmarks or phosphenes to determine stimulation sites, but such positioning methods are not accurate. Empirical evidence has indicated great individual differences in V5 locations, which could lead to stimulating a different brain area. In addition, phosphene-based positioning can be

problematic too, because only a very small portion of subjects can perceive phosphenes [31], and V5 is not the only area that induces moving phosphenes [60]. For these reasons, further studies are necessary.

4. Conclusions

As we have indicated, visual awareness is a very complicated process. Dissociations between consciousness and other psychological phenomena have contributed to the overall understanding, and experimental exploration of feedback processing from higher cortical areas to lower ones provides an effective method for studying neural mechanisms of visual awareness. However, we are still far from a thorough understanding of visual awareness, and further efforts must be made. First, there are still discrepancies between studies; none of the theories put forth as of yet can explain all results. Second, in addition to the cortex, many sub-cortical structures have been shown to be related to consciousness, such as the lateral geniculate nucleus (LGN) [61], superior colliculus [62] and intralaminar nuclei (ILN) [63]; their roles in visual awareness remain unclear. Finally, the role of V1 in feedback processing is not completely understood; the terms “binding”, “amplifier”, and “look-up table” are only vague analogies. Taken together, the quest for understanding highest and most complex psychological phenomenon “consciousness” has only just begun.

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