Trends in Cognitive Sciences

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What's next? New evidence for prediction in human vision

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Everyday visual experience involves making implicit predictions, as revealed by our surprise when something disturbs our expectations. Many theories of vision have been premised on the central role played by prediction. Yet, implicit prediction in human vision has been difficult to assess in the laboratory, and many results have not distinguished between the indisputably important role of memory and the future-oriented aspect of prediction. Now, a new and unexpected finding – that humans can resume an interrupted visual search much faster than they can start a new search – offers new hope, because the rapid resumption of a search seems to depend on participants forming an implicit prediction of what they will see after the interruption. These findings combined with results of recent neurophysiology studies provide a framework for studying implicit prediction in perception.

What's next? New evidence for prediction in human vision

The next time you hear familiar footsteps outside your door, pay close attention to your visual experience when the person appears. If your prediction is confirmed, you will fluently identify the person and begin your social exchange. But if those footsteps belong to an unexpected person, albeit one familiar to you, you will do a double-take. Your visual identification will be momentarily frozen by the mismatch between your auditory-based prediction and the person's appearance.

Analogs of these everyday experiences are being studied in cognitive laboratories. For example, simply hearing the characteristic sound of an object improves a search (e.g. hearing a jingle while searching for keys) even though it carries no location information [1]. Implicit predictions also seem to contribute to the experience of a colored and wide-angled field of view. Research with scenes that have been altered to remove color from some regions (Figure 1) indicates that viewers often fail to experience a reduction in color appearance, provided that the natural texture of the region has not been disturbed [2]. The tendency of the brain to predict color from learned associations might sustain the useful illusion of a world rich in color, when in fact our actual color sensitivity in the visual periphery is very limited.

The inherently predictive nature of perception has long been recognized in theory [3–6]. Indeed, the term 'analysis by synthesis' was coined to express the idea that perception involves an iterative exchange between sensation and cognition, with cognition seeking confirmation of its hypotheses in the sensory data [7]. Yet at the same time that the theoretical case was being made, it was considerably more difficult to find evidence for visual prediction in the laboratory. To appreciate this point, note that prediction implies more than the mere influence of experience. Memory of the past does not in itself imply a future-oriented prediction. It is one thing to be capable of visual prediction when necessary (Box 1) but quite another to be making predictions when they are not formally required.

Consider priming, which is the increase in efficiency of responding to an image (or a very similar image) for a second time [13–15]. Priming can be interpreted as the brain predicting something about the future but such an interpretation is not required. The first image might simply have made a lasting impression that is more readily accessible when the second image appears [16–18]. Eye movement studies also fall prey to this ambiguity [19–21]. After an initial glance at a scene, do the eyes move to a location because the visual system predicts something [22,23] or do familiar associations guide them [24]? Even the flash-lag illusion – the misperception of a moving object relative to a briefly flashed one – was initially presented as definitive evidence for visual prediction [25]. Yet it has since been reinterpreted in ways that no longer depend on the prediction [26–28]. Only in the area of visually guided action is the concept of prediction firmly established in theory and behavior (Box 2).

Recent developments in the neurobiology of predictive vision

Despite this ambiguity, there is renewed interest in perceptual prediction, which has been driven by studies of brain imaging in humans and electrophysiology in animals. These studies reveal that the time course of brain activation does not follow the conventional anatomical hierarchy [33,34]. Some higher-level cortical areas receive signals from the eyes at the same time, or even before, some so-called lower-order areas. Other studies show that communication between two brain areas is generally a two-way street, an arrangement known as recurrent signaling [35,36].

Box 3 and Figure 2 summarize many of the common features of theories inspired by the new neurophysiology [37–42]. These include (i) a distributed anatomical hierarchy, involving the convergence of low-level units (typically registering local features that are spatially specific)

Figure 1. (a) An original full-color image. The same image after alteration to include: (b) a central region with no color, or (c) peripheral regions with no color. Viewers often fail to notice the missing color, provided the natural texture of the altered regions has not been disturbed. Reproduced, with permission, from Ref. [2].

on to a smaller number of higher-level units that are linked to stored knowledge (typically coding more abstract features with reduced spatial specificity) and (ii) multiplexing, referring to the fact that neurons change their response properties over time as they are influenced by feedforward, feedback and resonant patterns of firing.

In short, the new neurophysiology reveals that what we colloquially call perception involves three distinct phases: activate (feedforward sweep), predict (feedback sweep) and confirm (stable state of resonance). Studies of visual surprise (Box 4) are consistent with the position that seeing is fluent and efficient only when the first two phases (acti-

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Box 1. Visual tasks requiring or evoking explicit prediction

The present article focuses on predictions made implicitly by the visual system in the course of ordinary perceptual experience. But in considering this question, we must not lose sight of the fact that there are many visual tasks that can be accomplished only by having the viewer make an explicit prediction. One example is a motion perception task requiring a judgment of 'time to collision' [8]. These studies show that humans have finely tuned mechanisms for detecting the future winner in a race involving two objects in motion [9], for detecting future collisions among objects in motion [10] and for detecting the moment of impact for collisions of moving objects with themselves [11].

When it comes to making predictions about possible collisions between ourselves and other objects, we might not even be able to turn off this tendency. For example, in one study viewers performed a search task in which one object in the display increased in size abruptly just before the onset of the search [12]. Importantly, there was no correlation between the location of the looming object and the target. Yet, the attention of viewers was drawn involuntarily to the looming object, particularly when the future point of implied collision was with the head or torso of the viewer. This finding demonstrates that visual predictions are sometimes made even when they are not formally required.

vate, predict) have been completed in advance of the final phase (confirm).

Unexpected finding offers new evidence of prediction in vision

The recent finding of a unique pattern of search behavior in humans promises a way, from within this predictive-brain framework, to study implicit visual prediction. The main result is that we can resume a previously interrupted search much faster than we can start a new search [49]. The evidence for prediction – versus merely fluent access to memory – is based on two crucial findings. The first finding is the sheer speed with which a search can resume after an interruption. Correct responses in a difficult serial search task occur within 200–300 ms of the re-presentation of the search display. Given that all previous studies of search tasks that showed benefits of visual priming and short

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Box 2. Prediction in human motor action

Predictions in human motor action have been studied for a much longer time and have more strongly established theories than have implicit visual predictions. Theories of human motor control use the term forward model to describe predictions. The predictions are models, because they involve the construction of simulations that are internal to the brain. They are forward because they make predictions about future actions, permitting the consequences of these actions to be tested before their execution [29].

For example, in the classic size–weight illusion, lifting up the smaller of two identically weighted objects seems to take more effort than lifting up the object that looks larger. The brain makes different motor predictions for the two objects based on their visual appearance. When these predictions are violated during the lift, the smaller object is perceived as heavier [30]. The precise timing of motor predictions can be studied in the unloading task, which involves lifting a weighted object held in one hand by a second hand [31]. When the lifting and holding hands belong to the same person, the muscles of the holding hand undergo a decrease in activity that is precisely timed with the lift, resulting in a steady holding hand as the object is lifted off. But when the lifting hand belongs to another person, the prediction about when the lift will occur is less accurate, and so the holding hand involuntarily rises as the weighted object is lifted off [32].

Box 3. The perception cycle

The three panels in Figure 2 illustrate phases of activity for visually sensitive neurons, as they might respond during the everyday task of identifying your keys. The cycle begins with activation of neurons (red arrows and boxes) that are sensitive to the visual features associated with 'my keys.' But the activate phase by itself is not sufficient for vision because several crucial functions are incomplete. First, memory neurons that recognize a particular object (e.g. my car keys) might not be activated exclusively; neurons that recognize other keys might be active as well. Another ambiguity concerns where these keys are located in space. Because receptive fields of higher-level neurons are large, these neurons are unable to signal the precise location of the image features that gave rise to their activation. A final uncertainty concerns the source of their activation. Did memory neurons recognizing 'my keys' become active because I imagined them (feedback signals from memory neurons) or because I actually saw them (feedforward signals from the eyes)? Thus the activate phase might generate hypotheses about what I am currently seeing, but it is unable to confirm many details about the source of this activation.

Progress in resolving these ambiguities is made in the predict phase (blue boxes and arrows). Given 'my keys' neurons have won the competition for the most likely source of activation, this information is broadcast down the hierarchy in search of confirmation and more detailed location information. If this feedback sweep is in agreement with the activity at the lower levels, confirmation can begin. If not, a new hypothesis must be generated.

When the feedback sweep finds agreement at the lower levels, ambiguities remaining from the activate phase can be resolved, which leads to the confirm phase of the cycle (green boxes and arrows) and ultimately conscious perception of 'my keys.' The first two phases, although crucially important to seeing, are inaccessible to our experience. Only the confirm phase results in the conscious experience we normally associate with seeing [38–40].

Box 4. Surprise! Delayed perception of unexpected events

Some events grab our attention even when they are irrelevant to our current goals. It is often assumed that such surprising (i.e. unpredicted) events capture our attention most completely, but this must be reconsidered in the light of evidence that surprising events are actually processed inefficiently. Research on inattentional blindness directly addresses this point; unexpected events can go completely unnoticed if attention is not drawn to them by some means [43].

One series of studies examined the influences of suddenly appearing, task-irrelevant events that were either totally unexpected or expected, but equally rare in both cases [44,45]. The results showed that unexpected rare events exerted their influence more slowly than did expected rare events. It seems that events inconsistent with a prevailing schema or expectation can alert the brain to a discrepancy, but the actual identification of unexpected events is slow and inaccurate because the perception cycle has to begin again with a new hypothesis (Figure 2).

This is also the conclusion to a controversy about an effect called novel pop-out, which at first appeared to show that an unusual item automatically attracted attention when displayed among familiar items [46]. Careful study of the methodology of these studies, however, revealed that they were inappropriate for indexing the rapid orienting of attention [47], and direct tests of the speed of orienting to familiar and unfamiliar items showed that participants who responded most rapidly showed a familiarity orienting bias, whereas only those participants responding more deliberately showed a novelty orienting bias [48].

term memory have elicited responses that begin ~500 ms after the onset of a display, correct responses that are as fast as 200–300 ms call out for a new explanation. The second finding is that whether rapid responses are possible depends crucially on whether participants are able to form a perceptual prediction during the interruption of their search and to confirm that prediction when the search resumes.

Rapid resumption was first observed when viewers were given the task of searching for a T among L-shapes (Figure 3a). The only unusual aspect of this search was the occasional interruption. Viewers were given brief presentations of the search display (i.e. 'looks') separated by longer interruptions (i.e. 'waits'), and when they found the T they pressed a key to indicate its color. Color was not a clue because half of all items were blue and the other half were red.
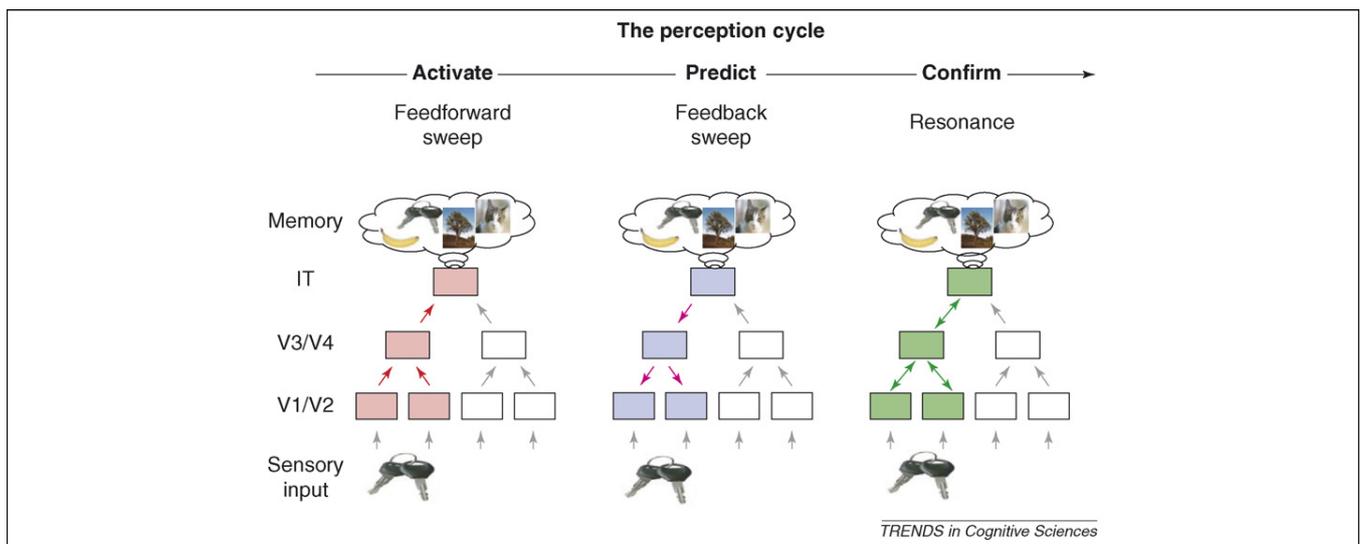

Figure 2. The perception cycle for identifying your keys, as described in Box 3. Although the levels of the anatomical hierarchy are labeled with brain regions involved in object perception, an analogous scheme would apply if we focused on motion or face perception. In the present example, V1/V2 represents the primary visual cortex with its local sensitivity to color and edge orientation, V3/V4 refers to extra-striate regions that are sensitive to shape and surface properties, and IT represents the inferotemporal cortex, where neurons respond to object identities and their functions.

Viewers were easily able to find the target within a few presentations of the display. The surprise finding was the many extremely fast responses after display re-presentation. Figure 3b shows a distribution of all correct responses made after six successive exposures, separated by 1 s blank intervals. After the first presentation, the vast majority of these responses occurred in the second half of the epoch, that is, after 500 ms had elapsed. However, after the second presentation, and again after each subsequent presentation, responses began at 200 ms. Our detailed analyses revealed two distinct periods in the responses after interrupted presentations: an early period of responding with a peak at 200–300 ms and a later period with a peak near 600–700 ms. To confirm that these two periods index different aspects of perceptual activity, we varied factors that might influence each period independently. When this dissociation was successful, we defined rapid resumption as responses made in less than 500 ms. This demarcation is admittedly arbitrary, but it serves to divide

an early from a later period of responding that is influenced by different factors.

What we think is going on in the perception cycle during an ordinary search is that before even seeing the display viewers activate a short-term memory of the target image [50,51]. After a few trials of searching for the T, viewers have formed detailed representations of the target in its various orientations and colors. Yet, note that a first glimpse of the display still rarely elicits a response in less than 500 ms. Why does it take so long? The perception cycle suggests that even when the viewer's eye is presented with the target, it is still necessary to activate and test a hypothesis about it (i.e. to distinguish it from mere memory), to confirm that this match is sufficiently strong to achieve a resonant state (i.e. to consciously see it) [38–40] and to prepare a motor response.

If all this takes about 500 ms, how is rapid resumption able to escape some of these time-consuming steps? We propose that these responses are an index of the activate
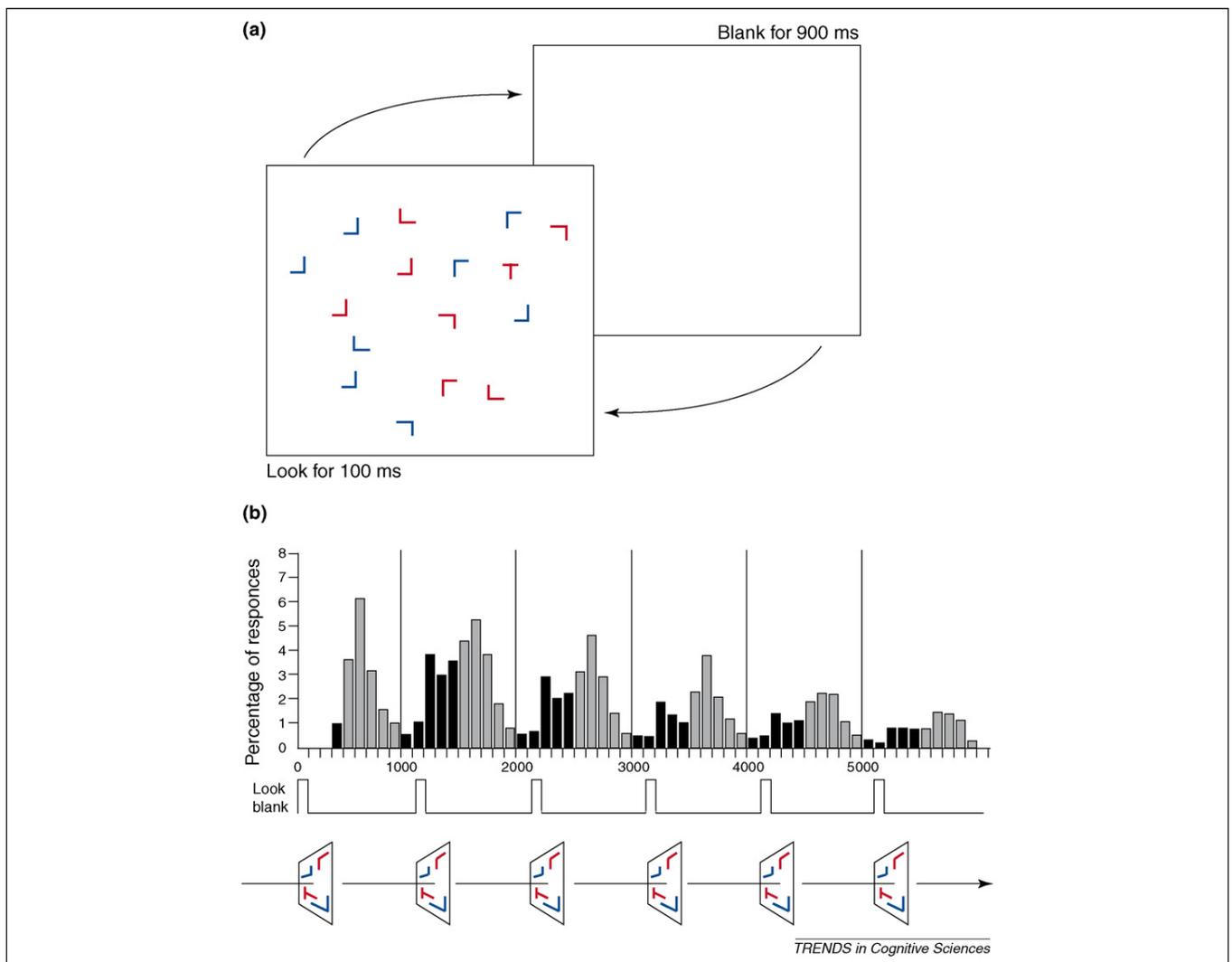

Figure 3. **(a)** Illustration of an interrupted search task in which rapid resumption can be observed in the pattern of correct responses over time. Participants search for a T-shaped target among L-shaped distractors. They indicate that they have found the target by pressing one of two keys to indicate its color (blue or red). The only difference between this and previously studied search tasks is that the search involves brief looks at the display that are interrupted by longer waits. **(b)** The distribution of all correct responses made after six successive looks, separated by 1 s waits. Almost all responses after the first look begin after more than 500 ms have elapsed. However, on the second and subsequent looks, responses begin at 200 ms and are distributed with two distinctive peaks. We refer to the responses made in less than 500 ms after a look as rapid resumption.

and predict phases being initiated by one look, and the confirm phase has to wait for the reappearance of the display before neural resonance is sufficient to generate a conscious experience of the target [38–40]. In short, rapid resumption is evidence that viewers have formed a prediction in one glance; but this prediction requires confirmation with sensory evidence to result in perception. The crucial insight is that performing only the confirmation phase when the display reappears takes less time than beginning the cycle anew.

The hypothesis that rapid resumption is an index of prediction has been tested in several ways. We began by noting that prediction owes its utility to the assumption of a stable world. Correspondingly, rapid resumption was eliminated when the target location shifted between looks [49], even when a gaze-contingent viewing procedure was used, such that no matter where the viewer looked, the target was presented to the center of gaze on every look [52]. In other experiments, we examined the well-known finding that search time increases along with the number of candidate target items (i.e. a display size effect). Display size effects are diagnostic for gauging the extent to which a search is limited by attention, and larger effects corresponded to stricter capacity limits [50,51]. We reasoned that if rapid resumption is an index of an implicit prediction, it should be immune from display size effects because a confirmed prediction is required to see the target, regardless of the complexity of processes undertaken in advance. This is what we found: more items in a display delayed the epoch in which the target was found but had no effect on the distribution of responses within an epoch [49].

A direct way to test whether rapid resumption is an index of implicit prediction, compared with only a benefit of past experience, is to see whether viewers can make a correct response when the display fails to reappear. They could not [49]. In a related experiment, half of the first looks given to viewers included everything in the complete search display with the exception of the target [53]. The results were clear: presenting the entire display with the target absent in the first look was not sufficient to yield rapid resumption when the target appeared on the second look. Thus viewers were probably not making a prediction about the overall scene, but rather about a specific region or object in it.

The factors examined thus far have all reduced the likelihood of rapid resumption by undermining the viewer's ability to make a prediction. By the same logic, there should be factors that increase this behavior. When viewers see displays for 500 ms rather than for 100 ms, which increases the likelihood of activating a prediction, the relative frequency of rapid resumption is increased [49]. Guiding the viewer's spatial attention either by placing the target at the center of the viewer's gaze [52] or with a cue that correctly predicts the location of the target [54] also increases rapid resumption. But crucially, this does not occur on the look immediately after the guided fixation or the cue. It is only on the second look after these procedures that rapid resumption is increased. In other words, attending or looking where the target is going to appear is insufficient to produce rapid resumption, because even in these best-case scenarios, the perception cycle begins

from scratch. By contrast, having attended or looked at the target location in advance increases the likelihood that the activate and predict phases have already occurred, increasing rapid resumption responses on subsequent looks.

Concluding remarks: the future of implicit perceptual predictions

We have interpreted the finding that humans can resume an interrupted search much faster than they can start a new search [49,52–54] as evidence that implicit predictions are formed in the course of everyday visual behavior, such as finding your keys on a cluttered desk. But questions remain (Box 5), and there is much work to be done, both to confirm that the rapid resumption of a search really involves forward-acting perceptual predictions and then to study the nature of those predictions to understand better their underlying function and neural representations.

An important theoretical alternative to the perception cycle framework (Figure 2) is the possibility that success in an interrupted search depends on the simple accumulation of evidence in favor of one response over the other. Perhaps the information in a look adds to this evidence even when it is insufficient to trigger conscious perception. When some threshold is reached, after the second or third look, conscious perception ensues. By analogy, a partly filled rain gauge need not make an advance prediction to overflow during the next storm.

We believe that the processes underlying rapid resumption are different from those implied by a passive accumulator model. First, pilot data from our laboratories indicate that whether rapid resumption occurs with a given set of displays depends on the strategy adopted by the participant; if the participant chooses to consider each look a new event, rather than a repeating display, rapid resumption is abolished. Second, other pilot data indicate that the formation of explicit expectations about a target (i.e. priming the accumulator with conscious imagery) is also not sufficient to produce the fast responses distributions of rapid resumption; implicit expectations based on viewing the

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Box 5. Outstanding questions

1. What are the similarities and differences between the implicit predictions made by the brain in the service of conscious visual perception and those made during visually guided action?
2. What roles are played by display crowding (i.e. increased spatial density of items) as distinct from display visibility (i.e. reduced contrast of display items from their background) in leading to the implicit predictions indexed by the rapid resumption effect?
3. What is the role of strategy in the rapid resumption effect? Specifically, what psychophysical procedures might be able to isolate failures to observe rapid resumption due to viewer inactivity (e.g. viewers using a sit-and-wait strategy) from an inability to form a hypothesis (e.g. insufficient display visibility)?
4. Is an implicit prediction formed on the basis of information in one sensory modality (e.g. audition) capable of permitting rapid resumption of a search in another sensory modality (e.g. vision)?
5. Do the fast responses indexed by rapid resumption occur specifically when the confirmation stage of the perception cycle is complete, or does the process of confirmation occur during the wait between looks, thereby enabling a faster activate phase on the subsequent look?

target (even though not consciously) are much more effective. But further direct tests, ideally involving competing predictions of accumulator and predictive theories, are needed.

If the predictive interpretation is sustained, rapid resumption will open up new ways to study the unconscious mind. The evidence so far implies that predictions made during a search are specific to the location and identity of the target, but it does not specify which features are involved and how much local context is included. These questions are being addressed with experiments reminiscent of those used to study change blindness [55], in which the ability of participants to detect a display change from one look to the next is used as an index of the internal representations they have formed. As in those experiments, displays alternate between looks, but instead of asking viewers to give an explicit report of detecting a change, we test whether the changes influence the implicit processes of rapid resumption. One study of this type reported that rapid resumption still occurred when an incidental feature changed from look to look, but it was much reduced when response-relevant features changed [53]. A similar strategy was used to test the representation of the local target neighborhood [56]. Rapid resumption was reduced by changes in distractors near the target, but not in those more distant from the target.

One of the most intriguing features of rapid resumption is its implicit nature. Participants seem unaware of whether a given response is from the early or the later peak of the response distribution, or of the specific contents of the prediction they are making [49,53]. This lack of self-awareness indicates that the cognitive mechanisms most often associated with consciousness (i.e. visual working memory, executive attention [57,58]) might not be involved in the on-line control of the activate and predict phases of perception. If not, participants should be able to engage working memory with an unrelated task while rapid resumption occurs in a simultaneous search task [59]. This hypothesis is under active investigation in our laboratories and shows promising results [60,61]. In a related study, we are testing whether large individual differences in search efficiency [62] have any influence on the prevalence of rapid resumption responses. It is our hope in writing this article that others too will begin to explore the implications of the rapid resumption phenomenon.

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