The distinct modes of vision offered by feedforward and recurrent processing

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An analysis of response latencies shows that when an image is presented to the visual system, neuronal activity is rapidly routed to a large number of visual areas. However, the activity of cortical neurons is not determined by this feedforward sweep alone. Horizontal connections within areas, and higher areas providing feedback, result in dynamic changes in tuning. The differences between feedforward and recurrent processing could prove pivotal in understanding the distinctions between attentive and pre-attentive vision as well as between conscious and unconscious vision. The feedforward sweep rapidly groups feature constellations that are hardwired in the visual brain, yet is probably incapable of yielding visual awareness; in many cases, recurrent processing is necessary before the features of an object are attentively grouped and the stimulus can enter consciousness.

OUR UNDERSTANDING of vision has advanced considerably by subdividing it into distinct processes. For example, the distinction between spatial and object vision has been related to distinct neural pathways in the brain[1]: a dorsal stream that relays visual information to the parietal cortex, and a ventral stream that projects to the temporal cortex (Box 1). A second major dichotomy is between attentive and pre-attentive vision. Pre-attentive vision operates on an entire visual scene, in parallel to segregate visual objects from the background. This only works, however, if the object differs from the background in one or several elementary features. If these elementary feature differences are not available for segregation, the scene has to be inspected in a more serial manner; this is the domain of attentive vision[2–4]. A third dichotomy under consideration is between conscious and unconscious visual processing. We experience vision mostly through our conscious percepts. However, a visual stimulus that bypasses visual awareness can also be transformed into a motor output. This not only happens in pathological conditions, such as blindsight[5], but has also been demonstrated in normal subjects[6].

With the recent advances in neuroscience, we are also beginning to understand the dichotomies, attentive–pre-attentive and conscious–unconscious, in neural terms. For example, in the pre-attentive–attentive dichotomy it has been suggested that specific neural circuits, in particular in the parietal and prefrontal cortex, are involved in attentive vision[7,8], whereas low-level retinotopic areas are involved in pre-attentive vision[3,9]. Similarly, the segregation of visual pathways into a ventral and a dorsal cortical stream has been suggested to underlie the distinction between conscious perception and visually guided action that can bypass consciousness[6,10].

An aspect of cortical processing that has been relatively overlooked in these models are the differences between the various types of connections in the visual cortex[11]. Feedforward connections relay information from lower to higher visual cortical areas, but there are also horizontal, within-area and feedback connections. Edelman[12] was among the first to suggest that these 're-entrant' connections play a prominent role in a variety of visual functions. Here we will try to relate the distinction between connection types to functional dichotomies in visual processing.

The fast feedforward sweep of information processing

After the presentation of an image, the successive hierarchical levels of the visual cortex are rapidly activated through the cascade of feedforward connections. This is what we call the feedforward sweep of information processing. Activation spreads from low-level to high-level areas of the visual cortical hierarchy[13]. Anatomically, V1 is the lowest visual area, in which information has to cross at least two populations of synapses (in layers 4C and 2–4B)[14] before it can reach higher areas. The stream of information bifurcates into a dorsal and a ventral stream. In the ventral stream, areas of the temporal lobe are thought to be at the top of the visual cortical hierarchy. In the dorsal stream, the top is more difficult to accurately define. The hierarchy that is based on corticocortical connections fits well with hierarchies that are based on physiological criteria, such as the increase in receptive-field size and the complexity of tuning properties in higher visual areas[15] (Box 1).

A more direct way of characterizing the feedforward sweep is by an analysis of the latency of visual responses in the cortical areas (Box 2). This yields a somewhat different picture than that expected on purely anatomical grounds. For example, cells in area MT and the frontal eye fields (FEF) areas are activated almost as rapidly as cells in area V1. There are several reasons for the non-correspondence between this temporal and the anatomical hierarchy (see Box 2).

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Box 1. Anatomical organization of the visual system

The organization of the visual system has parallel as well as hierarchical features. Several parallel pathways (magno-, parvo- and koniocellular) can be discerned that transfer different kinds of information from the retina to the LGN and cortex. In the cortex, these pathways are recombined. Functional subdivisions in areas V1 (blob and interblob regions) and V2 (thick, thin and interstripe regions) have been defined on the basis of cytochrome oxidase (CO) staining. After the recombination, two pathways emerge: a dorsal, magno-dominated pathway flows to the parietal cortex and is mostly involved with space, movement and action and a ventral, parvo-dominated pathway flows into temporal areas and is mostly concerned with object identification and perception[a] (Fig Ia,b). Three connection types can be identified within this parallel flow. Those that provide input from cells at lower levels (feedforward connections), those that provide input from cells at the same level (horizontal connections), and those that provide feedback from higher levels (feedback connections)[b] [Fig. Ic, part (i)]. Feedforward connections shape the classical receptive field (cRF). The cRF corresponds to the region of the retina to which a neuron is connected by way of feedforward connections.

The cRF increases in higher areas and tuning becomes more complicated [Fig. Ic, parts (ii), (iii)]. Through longer routes, which involve hori-zontal and feedback connections, neurons also receive information from the surround of their cRF [Fig. Ic, part (ii)]. Feedforward, horizontal and feedback connections have different layers of origin and termination. These differences have been exploited to define a hierarchical scheme in which the relative hierarchical positions of most visual areas match the type of interareal connections[c].

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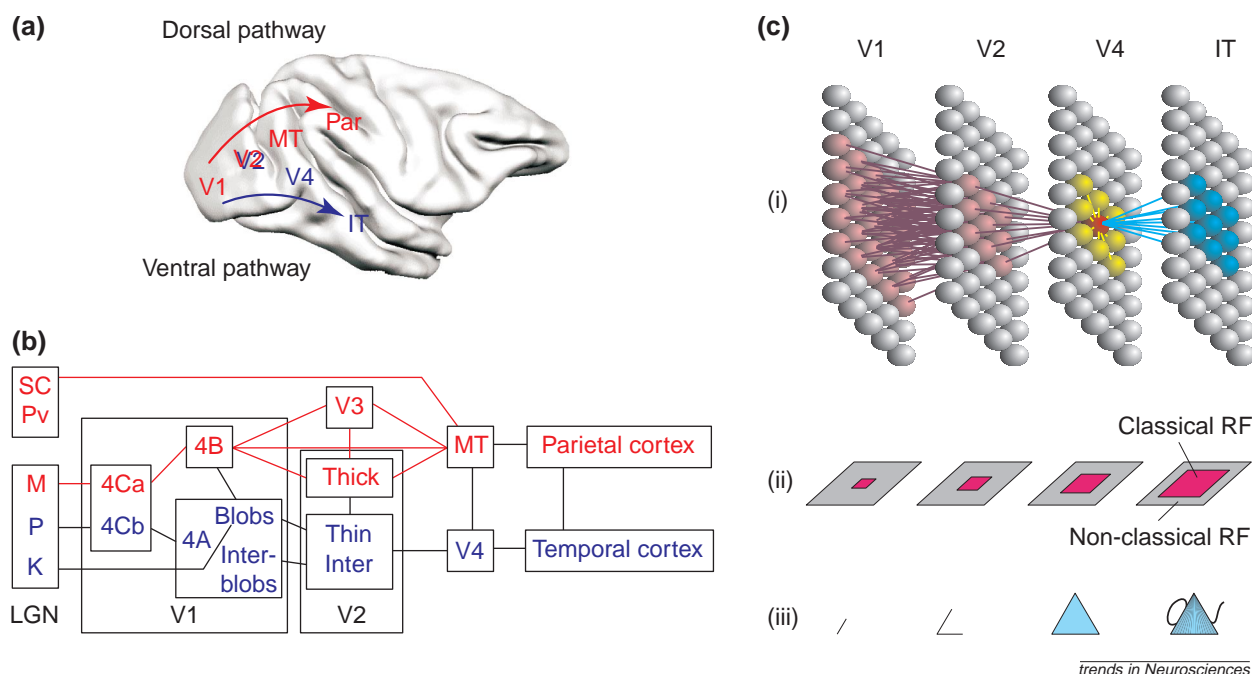
Fig. I. *Anatomical connections and receptive fields. Anatomical connections are shown at three different levels of detail. The two cortical streams are shown in an MRI image of monkey cortex rendered with BrainVoyager© software* **(a)**. *The interareal connections of the early visual areas and the segregation of these connections according to LGN input and cytochrome oxidase (CO) staining are shown in* **(b)**. *Components of the magno-dominated 'fast brain'[d] have been shown in red. This system includes a connection from the superior colliculus (SC) and Pulvinar (Pv) to area MT.* **(c)** *Part* (i) *representation of feedforward (pink), hori-zontal (yellow), and feedback (blue) connections to a hypothetical neuron in V4 (red). The increase of receptive field (RF) size is shown in part* (ii), *and the increase of the complexity of receptive field tuning properties is shown in part* (iii), *going from low-level to high-level areas[e].* (a) *MRI image courtesy of R. Goebel and N.K. Logothetis.*

Furthermore, large differences exist between latencies of dorsal and ventral stream areas because of the different speeds of the magno- and parvo-pathways feeding into these areas.

An important feature of the organization thus is that not one, but multiple parallel feedforward sweeps can be identified that operate at different speeds. Yet each of these sweeps share several important characteristics. First, they proceed rapidly. The exact speed depends on stimulus variables (e.g. contrast, motion, type of onset), but after the presentation of a high-contrast stimulus, the highest levels of the visual cortical processing hierarchy in the ventral stream are reached within 100 ms. Second, they are mainly determined by the feedforward connections. Response latencies at any hierarchical level are usually about 10 ms longer than those at the previous level. Thus, because 10 ms is in the range of the minimal interspike interval[16,17], a typical cortical neuron can fire at most a single spike before the next hierarchical level is activated, leaving little time for lateral connections and no time for feedback connections to exert their effect. Therefore, the ensemble of neurons that participate in the first sweep of activity through the hierarchy of visual areas is primarily determined by the pattern of feedforward connections.

These data imply that the degree of tuning of the first spikes provides an indication of what is
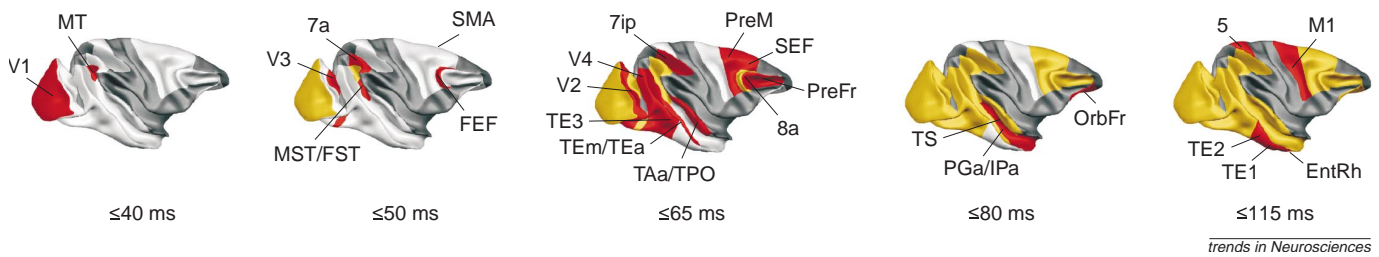
Box 2. The feedforward sweep

Fig. I. *Earliest visual response latencies of areas in the macaque cerebral cortex.* Activation of areas at specific latencies, shown in MRI images of monkey cortex, rendered with BrainVoyager® software. Areas that have become active at the given latency after visual stimulation are shown in red in each plot. Regions shown in yellow represent the areas that were activated earlier. White regions are not yet activated. Dark gray regions represent areas for which no information was obtained. Latencies of the layers of the LGN, magnocellular (earliest 28 ms, mean 33 ms) and parvocellular (earliest 31 ms, mean 50 ms) (Ref. c) are not shown. MRI images courtesy of R. Goebel and N.K. Logothetis.

An independent measure of the hierarchical level of a visual area can be derived from the latency of the responses that are evoked by a stimulus that appears suddenly. We peformed a meta-analysis (48 studies) of visual response latencies that have been reported for various areas of the visual, parietal, frontal and motor cortex of the macaque monkey. For some areas considerable discrepancies between studies were observed, which are presumably related to: differences in methods for the calculation of latency; differences between visual stimuli and differences in behavioral state. Moreover, in some studies only the median of the distribution of latencies is reported, whereas others only report the average latency. These factors cannot, however, contribute to differences in latencies between areas that have been studied by the same authors. Therefore in the meta-analysis, particular weight was attached to studies that compared latencies in two or more areas.

For each area A a latency λ_A was estimated by minimizing the following error term:

$$Err = \sum_{S,A} (\lambda_A - L_{S,A})^2 + W \sum_{S,A,B} F_S [D_{S,A,B} - (\lambda_A - \lambda_B)]^2$$

Here, $L_{S,A}$ is the latency in area A, and $D_{S,A,B}$ the latency difference between areas A and B, reported by study S. W determines the relative weight attributed to differences between latencies in areas that were examined in a single study. W was set to five in the present analysis. F_S is a normalization factor that avoids disproportionate weighting of studies that report latencies in more than two areas. A study that reports latencies in N_S areas contributes $N_S - 1$ independent estimates of interareal latency differences (degrees of freedom), but yields $0.5 \cdot N_S (N_S - 1)$ values for $D_{S,A,B}$. Therefore, F_S equalled $[(N_S - 1) / (0.5 \cdot N_S \cdot (N_S - 1)]$. The analysis was carried out twice, once for the earliest latencies (Fig. I, Table 1), and once for the average latencies (Table 1).

Several factors are responsible for the non-correspondence between this temporal hierachy and the topological hierachy of Box 1.

(1) Not all neurons within a given area receive their inputs via the shortest possible routes. Thus, the hierachy falls apart at the level of individual neurons. Indeed, a layer 4C neuron in V2 might be closer to visual input than a layer 5 cell in V1.

(2) The several streams of information processing that can be discerned have different speeds. The magnocellular pathway is fastest, followed by the moderately fast parvo- and the slow koniocellular pathway. Each pathway projects to different layers in V1, and from there to different pathways within V1 and beyond (Box 1). Thus, a neuron that is topologically close to the retina, but that belongs to a slower stream, might respond later than a neuron that is topologically further from the retina.

(3) The LGN is not the only source of visual information, because other subcortical structures, including the superior colliculus (SC) and pulvinar (PV), also project to various extrastriate areas.

TABLE 1. Visual response latencies in macaque cerebral cortex

Area	Earliest	Mean	Refs
V1	35	72	80–88
V2	54	84	84–86,89
V3	50	77	86
V4	61	106	82,86,90
TE3	57	109	91
TE2	83	123	91–94
TE1	86	143	91,95
TEm	59	114	91,96
TEa	59	123	91,96
Ipa	68	128	91,96
Pga	69	125	16,91,97
TPO	60	117	16,91,97
TAa	57	144	91
TS	67	139	91
TP	–	156	95
36	–	148	95
TF	–	146	95
35	–	175	95
EntRh	100	158	95,98
MT	39	76	82,85,86,99–102
MST/FST	45	74	86,99,100,103
7a	44	129	104–107
7ip	64	92	104,106
5	114	162	108,109
FEF	43	91	86,110–113
SEF	52	115	110,111,114
PreFr	51	141	106,114,115
8a	63	96	106
OrbFr	80	152	116
M1	85	150	109,117–120
PreM	57	127	109,114,119,121–123
SMA	48	124	120,124,125

Area MT, for example, receives an important input from the SC, that can sustain the responsiveness of MT cells in the absence of V1 (Ref. a). It has been argued that this pathway might provide visual input to the parietal cortex before the geniculostriate input has arrived[b].

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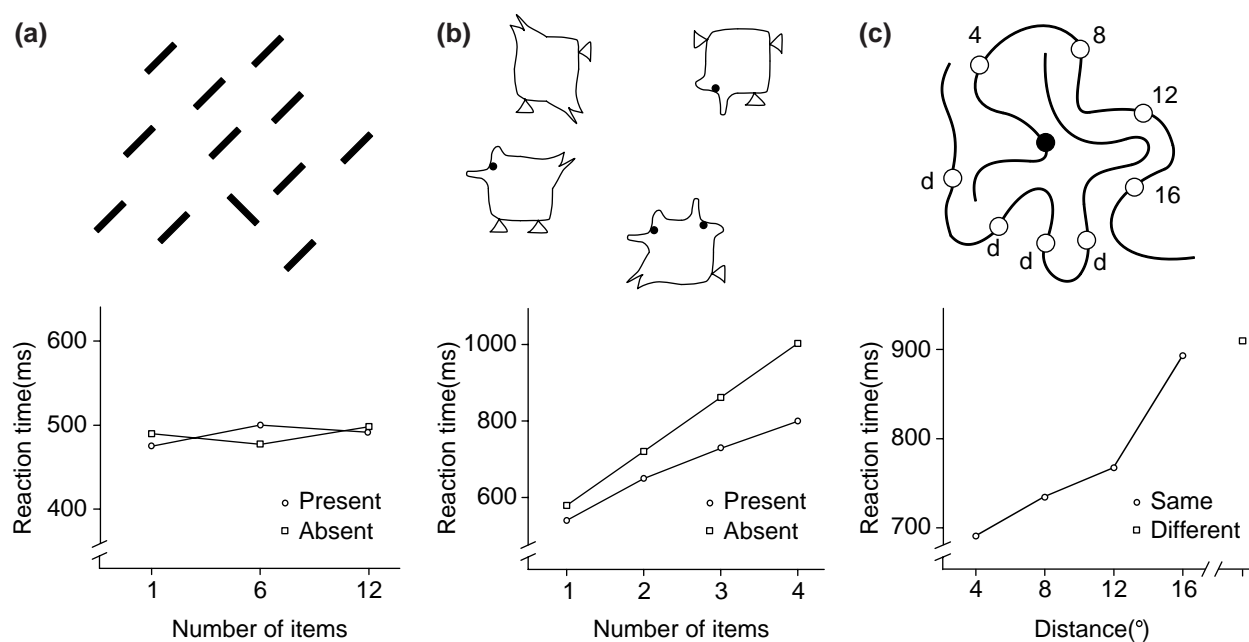
Fig. 1. *Visual tasks with differing demands on visual processing.* (a) *A visual search for an image element with a unique orientation is carried out in parallel across the visual field. The graph shows that the reaction time is hardly affected by the number of distractors. This type of search is also referred to as pop-out. Circles show reaction times in the presence, and squares in the absence of the target (modified from Ref. 28).* (b) *Search for a 'chicken' among distractors composed of chicken parts. Reaction times show a steep increase with the number of distractors (modified from Ref. 4). Circles show reaction times in the presence, and squares in the absence of the target. The original data were kindly provided by J.M. Wolfe.* (c) *A curve-tracing task[46], in which subjects had to indicate whether the fixation point (filled circle) was connected to a circular target, which could appear at one of a number of positions (unfilled circles). The target could appear on the same curve as the fixation point at a distance of 4°, 8°, 12° or 16°, or on the other curve d. During the actual experiment the target appeared only at one of these eight possible locations. In the graph, circles show the dependence of reaction time on the distance between the fixation point and target. The square indicates the reaction time in trials in which the target was on the curve that was not connected to the fixation point.*

achieved by feedforward connections, in terms of neural computation. The first spikes are remarkably selective in many cases that have been studied. For example, orientation tuning of V1 cells is present in the first spikes that can be recorded[18]. Similarly, the first spikes in the inferior temporal cortex exhibit tuning to complicated stimuli such as faces[16,17,19], and the first spikes evoked in area MST, an area of the parietal cortex contributing to motion perception, are tuned to complex patterns of optical flow[20]. The feedforward sweep thus exposes the very impressive capabilities of the feedforward connections; they determine the neurons classical receptive field (cRF) (Ref. 21), and their basic tuning properties. Oram and Perrett[16], and Tovée[17] suggested that this implies that visual cortical processing is usually finished when the feedforward sweep of activity has been completed. This might however, only be true for a limited part of visual processing. We will argue below that many aspects of visual processing rely crucially on what happens beyond the feedforward sweep.

Beyond the feedforward sweep

Visual cortical neurons remain active after their participation in the feedforward sweep. This occurs in areas both at lower and higher hierarchical levels. At these longer latencies, information from horizontal or feedback connections can be incorporated into the responses. The contribution of these recurrent connections can be distinguished from the feedforward sweep on the basis of several criteria.

A first indication for the involvement of recurrent connections is a change in the tuning of a neuron over the course of its response. In the primary visual cortex (V1), for example, tuning for orientation[22] and color[23] changes dynamically during the neuronal response. Such dynamic changes in tuning have also been observed for neurons in the inferotemporal cortex that are selective for faces. The early part of the response of these neurons simply depends on whether the stimulus is a face or not[17]. However, a significant portion of cells also convey information about facial expression or identity, but only after an additional delay[24]. Also, in other cortical areas, the initial responses reflect sensory processing by the feedforward sweep, whereas responses at longer latencies correlate with more cognitive or behavioral aspects of sensory processing. In parietal areas, for example, aspects of perceptual decisions are expressed at longer latencies[25]. Thus, cortical neurons are not simple detectors for one aspect of the visual scene. Instead, lateral and feedback connections allow them to contribute to different analyses at different moments in time. Even in the motor cortex, early responses reflect sensory events, whereas responses at intermediate latencies reflect sensory-motor mapping rules, and late responses reflect the motor commands[26].

A second indication for the involvement of recurrent connections is the modulation of a cell's response by contextual information occurring outside its cRF. Indeed, if the cRF is defined as the region of visual space from which a cell receives information by

way of feedforward connections (Box 1), influences from outside the cRF depend, by definition, on recurrent connections. Many studies have documented that stimuli in regions surrounding the cRF might inhibit or enhance the response to an item that is presented within the cRF (Ref. 21). A remarkable property of these modulations is that they often correspond to psychophysical measures of the effects that the surrounding stimuli have on the saliency of the RF stimulus. For example, when similarly oriented lines surround a line segment, it will be less salient than when it is surrounded by orthogonal lines. Correspondingly, contextual modulation in area V1 results in a lower response for the first situation than for the second[27]. Similarly, contextual modulation has been shown to reflect perceptual pop-out[27] (Fig. 1a), perceived brightness[29], color constancy[30], and perceptual grouping[31]. Horizontal connections probably play an important role in the modulations related to grouping[32]. Furthermore, involvement of recurrent connections is suggested by the finding that many of these effects occur at some delay compared with the onset of the RF response[33], and that these effects depend on feedback from the extrastriate area V2 (Ref. 34).

There is substantial evidence for the involvement of recurrent connections in the visual task of texture segregation. Figure 2a, shows how V1 cells respond to the presentation of a textured figure overlying a textured background. In this case the contents of the cRF do not allow the neuron to decide whether its RF is on the figure or the background[35–37]. Thus, figural response enhancement is an influence from outside the cRF, which comes at an additional delay. Modulatory effects related to figure–ground segregation have been shown to depend on feedback from MT (Ref. 38) and other extrastriate areas[39].

A third indication for the involvement of recurrent connections in a visual task can be derived from processing times. The fast feedforward sweep of activity is completed within approximately 100 ms (Box 2). Recurrent connections have to be involved in those visual tasks in which longer delays are obtained. Here we will discuss two such tasks, visual search and curve tracing.

Visual search is the prime example of a task in which long processing times can occur. In a search task the subject has to find a target item within a variable number of distractors. Typically, the average reaction time exhibits an approximately linear dependence on the number of distractors. In difficult search tasks each distractor item might add more than 50 ms to the reaction time, and displays in which the reaction time is increased by more than 300 ms are not uncommon[2–4,40] (Fig. 1b). Physiological studies of visual search in monkeys has shown that neurons in various visual areas enhance their firing rate if the target item appears in their RF, instead of a distractor[41–44]. This response enhancement is delayed relative to the initial visual response to the onset of the search display, suggesting that it is mediated by recurrent connections. Indeed, the response enhancement is also found in early visual areas, including area V1, exemplifying an influence from outside the cRF (Refs 42,45).

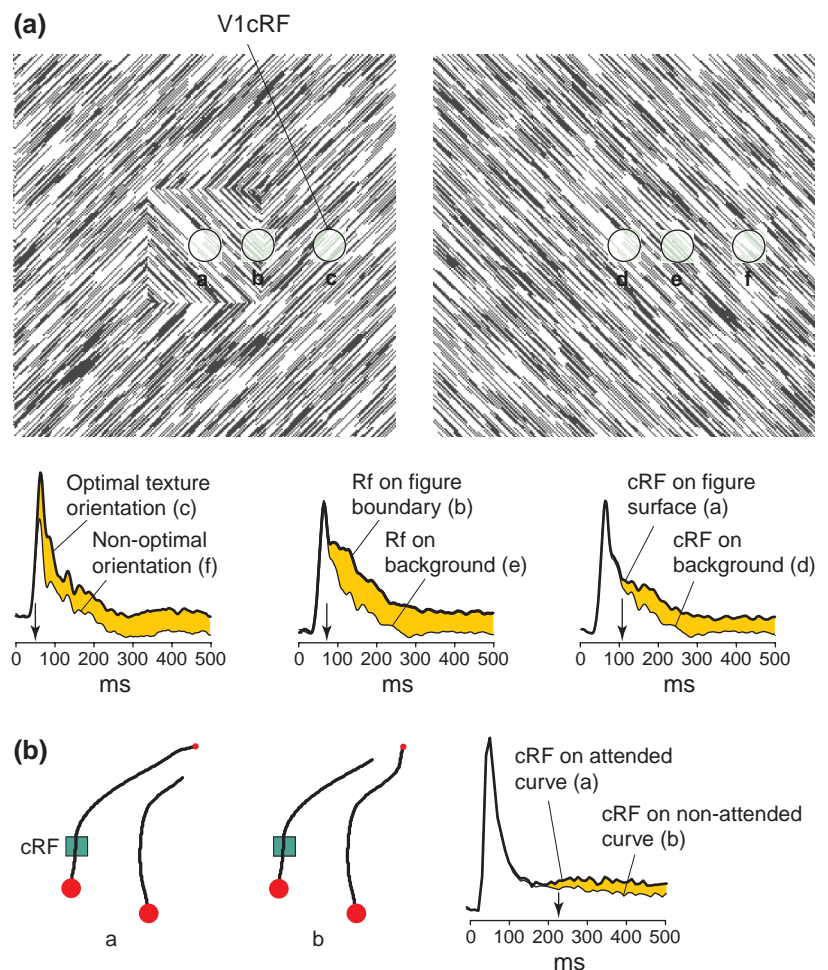In a curve-tracing task two or more curves are displayed, and the subject has to decide whether two

Fig. 2. V1 cells are sequentially selective for various aspects of a stimulus. (a) *Responses are compared with the receptive fields (RF) (circles, marked a to f) of V1 neurons at different locations of a texture. Comparing responses to differently orientated textures (c versus f, left graph, yellow shading indicates difference) shows that cells are selective for orientation of textures at 55 ms (arrow indicates moment of first significant difference). The same cells are selective for the boundary between figure and ground (b versus e, middle graph) at 80 ms, and show an enhanced response when the RF covers the figure surface compared to the background surface at 100 ms, even though the stimulus within the RF is identical in both situations[35] (a versus d, right graph).* **(b)** *V1 cells show a response enhancement by 30% if their RF is on a curve that needs to be traced, compared to when it is on a distractor curve. On average, the difference occurs 235 ms after stimulus onset[49].*

particular curve segments belong to the same or to different curves (Fig. 1c). The time to decide whether two segments belong to the same curve increases with their distance along the curve. This suggests that some time-consuming mental operation has to track along the curve to group all contour segments that belong to it[47,48], implicating the use of recurrent connections. We have recently recorded from the primary visual cortex of monkeys that were trained to perform such a curve-tracing task without moving their eyes[49] (Fig. 2b). Neural responses to the traced curve were on average enhanced by 30% compared with responses to a distractor curve even though the stimulus within the cRF was identical in both situations. The latency of the response enhancement was typically more than 200 ms. These findings indicate that the response enhancement is mediated by recurrent processing. Moreover, the response enhancement occurred for responses to all segments of the traced curve, even if it crossed another curve. This suggests that the entire cortical representation

of the traced curve 'lights up' during this task. We have proposed that labeling of neuronal responses by the rate enhancement might serve to bind the various segments of the traced curve into a coherent representation[50,51].

The above examples all suggest that recurrent processing typically exerts its influence at relatively longer latencies. However, some areas in the dorsal stream, such as MT, are activated at very short latencies, probably by fast subcortical and magnocellular pathways (Boxes 1 and 2). This would enable feedback from these areas to reach the early areas, such as V1, at about the same time as the feedforward input from the slower parvocellular pathway[9]. Indeed, cooling-experiments have shown that feedback from MT influences V1 responses very early on[52]. Such results illustrate how the interpretation of feedforward and recurrent processing is complicated by the non-correspondence between the anatomical and temporal hierarchy of corticocortical connections (Boxes 1 and 2).

The contribution of feedforward and feedback processing to pre-attentive and attentive vision

The hypothesis that visual responses are enhanced in order to integrate them into a coherent representation is reminiscent of the feature integration theory of Treisman and co-workers[2,3]. In this psychological theory, it is suggested that attention needs to be directed to an object in order to bind all of its features together. Rate enhancements have been widely reported as a neural correlate of visual attention[53] and appear to provide the neural mechanism of attentive grouping. During visual search, responses that are selective for the identity of the target item, as well as for its location, are eventually enhanced. Thus, attention labels the identity and location of the target item. During curve tracing, attention is directed selectively to the various segments of the curve that is traced[54]; attention appears to spread along the traced curve from segments that are attended, to new segments that are collinear and connected to them. Such a selective attentional labeling can be implemented by a spread of the rate enhancement through the network of corticocortical connections in V1, because these connections predominantly interconnect neurons that are tuned to nearby and collinear contour segments[50,51].

These data suggest that labeling by attention involves recurrent connections, which would explain why it is time-consuming. It is therefore tempting to identify recurrent processing with attentive grouping. Pre-attentive processing, by contrast, could be identified with the feedforward sweep. This association appears to hold at a first approximation, but there are also several subtleties[50]. First, most psychological theories suggest that attention is always required to group complex feature combinations[2,3]. Physiological data indicate, however, that the tuning that is obtained during the feedforward sweep can be complex, in particular, at the higher hierarchical levels[16,17,19] (Box 1). This elaborate tuning of neurons also constitutes a form of grouping. For example, if a face-selective neuron is activated, the eyes, nose and mouth of the face are grouped together by the visual system. Does this imply that such complex feature constellations are invariably extracted during the feedforward sweep?

The answer to this question appears to be negative. When elaborate feature constellations are embedded in a crowded search display, the feedforward sweep is curtailed. This is caused by inhibitory interactions among the representations of multiple objects, which are particularly pronounced at the higher hierarchical levels[53,55]. Thus, the depth of pre-attentive encoding might depend on the number and spacing of display items. Studies on visual search use many display items and the uncovered pre-attentive features are relatively simple[2,3,40] (but see, for example, Refs 56,57). Other methods to investigate pre-attentive vision have used fewer display items. For example, priming studies probe the depth of encoding of unattended display items by studying their effect at a later time point. These studies have uncovered deeper, even semantic encoding of non-attended objects[58,59]. Therefore, grouping by the distribution of attentional labels might only be required if neurons that are selective for the requested feature constellation are not available, or remain inactive during the feedforward sweep[50].

A second intricacy in the identification of pre-attentive vision with the feedforward sweep is related to the general application of the term pre-attentive to grouping that is based on simple image features, such as orientation similarity and collinearity. The physiological data discussed above suggest that such grouping operations might also require recurrent processing. In the segregation of a texture on the basis of a difference in orientation (Fig. 2a), for example, it takes time before the rate enhancement spreads to the interior of the figural region, thereby labeling this region as a single coherent object. Recurrent processing and visual attention are also involved in curve tracing, although this corresponds to grouping on the basis of collinearity and connectedness, criteria that have previously been identified with the pre-attentive system[60]. The involvement of attention in grouping, on the basis of elementary features, is supported by recent psychophysical studies[61,62].

A third intricacy in the mapping of the feedforward sweep onto pre-attentive vision is related to the possibility of separating an instruction cue from a visual stimulus in time. In this case, the instruction cue can generate feedback to lower hierarchical levels before the actual stimulus appears, thereby altering the subsequent feedforward sweep. Early instruction cues have been shown to modulate visual responses in parietal areas as well as in the FEFs at early latencies[63,64]. Temporal delays that are associated with attentional processing are expected to be most pronounced if the instruction cue and stimulus array are presented at the same time.

Conscious and unconscious processing and the feedforward–feedback distinction

Several views exist with respect to the neural basis of the conscious–unconscious dichotomy in visual processing. The results obtained from patients suffering from a lesion of V1 have been pivotal in this. These patients report not to perceive anything, that is to be blind, yet are remarkably good at 'guessing' about many attributes of the stimuli presented in the blind field, a phenomenon called blindsight[65]. Therefore, they exhibit visually guided behavior in the

absence of visual awareness[5]. A possible explanation for the blindsight phenomenon is that an interruption in the flow of information towards higher areas, as a result of a V1 lesion, prohibits visual awareness. After a V1 lesion, visual information is still routed to parietal cortex through other projections, but cells in the ventral stream appear to be silenced[11]. These, and other neuropsychological considerations, led to the suggestion that visual awareness is mediated by the ventral stream, whereas the dorsal stream mediates unconscious action[6,10]. However, this model cannot explain why blindsight patients are also good at 'guessing' about the color or form of unperceived stimuli[65], features that are thought to be processed by the ventral stream (but see Ref. 66). Moreover, evidence from human blindsight patients indicates that unperceived stimuli evoke activity in ventral stream areas[67].

Instead of attributing visual awareness to specific areas or pathways, it might be useful to relate the conscious–unconscious dichotomy to the distinction between feedforward and recurrent processing. Masking experiments provide support for this approach. In backward masking paradigms, the presentation of a stimulus is rapidly (<100 ms) followed by a second stimulus, the mask. Such a mask strongly reduces the visibility of the first stimulus, in some cases rendering it fully invisible[68]. Accordingly, information that enters the visual system later in time can have large effects on the awareness of earlier stimuli.

A backward masked stimulus evokes initial transients at the appropriate latencies (Fig. 3) in low-level areas[69,70] as well as high-level areas[59,71–74]. However, if the mask follows the stimulus with a short delay (20 ms), a slight suppression in the number of spikes that are evoked during the feedforward sweep and their tuning has been reported[72–74]. Such an early mask presumably cannot catch up with the very first spikes of the feedforward sweep, but can affect responses that are still within the initial response transient. It has been argued that this accounts for the masking effect[72–74]. An alternative explanation is that the mask disrupts the recurrent interaction between higher and lower visual areas[75]. Stimulus information from higher areas, when fed back to lower regions, will 'clash' with mismatching mask responses in lower visual areas (Fig. 3). Such a model also readily accounts for the effectiveness of masks that are presented at longer stimulus onset asynchronies (for example, see Ref. 69).

These two masking models might be distinguished on the basis of data obtained with transcranial magnetic stimulation (TMS). In a TMS experiment, a magnetic pulse is used to silence a cortical region of a healthy volunteer for a short period of time. TMS pulses that are applied to early cortical areas (V1 and/or circumstriate areas), can impair visual perception of a briefly presented stimulus if they have the appropriate timing[76]. Early blockade of perception is obtained with pulses that are applied 30 ms before and until 50 ms after stimulus onset[77]. Such early pulses presumably disrupt the feedforward sweep. Remarkably, pulses applied between 80 and 120 ms after stimulus onset are also effective in blocking perception[76]. At that time, the feedforward sweep has reached the higher visual areas. The data therefore
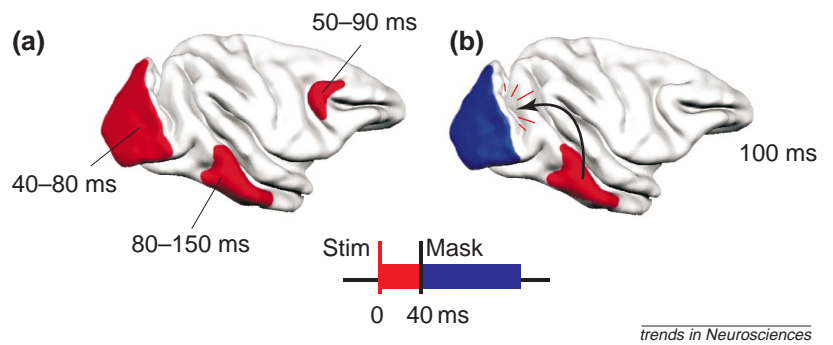

Fig. 3. *Masking interrupts recurrent interactions.* Neural activity was evoked by a stimulus lasting 40 ms (red bar), followed by a mask stimulus (blue bar). Psychophysically this typically leads to a strongly reduced visibility of the (red) stimulus. **(a)** The latencies of the response intervals of activity related to the 40 ms stimulus (not the mask) are shown for the areas V1, frontal eye field (FEF) and IT shown in red (Refs 69–74). This shows that the feedforward sweep is left relatively intact by the mask. **(b)** The effect of masking might be explained by the mismatch of recurrent information and feedforward information: at 100 ms, areas in the temporal cortex are activated by the stimulus (red) and they send feedback towards the lower areas. However, at this stage, V1 is activated by the masking stimulus (blue) and the feedback no longer matches the low-level activity.

suggest that recurrent processing in early visual areas is, at least under some conditions, necessary for visual awareness. It might be, however, that recurrent processing is not required in all conditions. It remains to be determined whether recurrent processing is also required for the awareness of stimuli, such as faces, which appear to be identified during the feedforward sweep.

Concluding remarks

Our current view of cerebral processing is heavily influenced by the concept of hierarchies, and the notions of feedforward and recurrent processing depend on this. Several parallel streams of hierarchical processing exist that overlap in space and time. Therefore, it is extremely difficult to disentangle the contributions of feedforward and recurrent processing on the basis of a single criterion, such as anatomical connections or latencies. Nevertheless, they remain extremely useful concepts in our understanding of cortical processing, as we have tried to demonstrate here.

In summary, we propose that the feedforward–feedback dichotomy might greatly aid in understanding the differences between pre-attentive and attentive vision, and between unconscious vision and visual awareness. Findings reviewed here suggest that the feedforward sweep of information processing is mainly involved in pre-attentive, unconscious vision, whereas recurrent processing is required for attentive vision and visual awareness. Does the overlap of the neural substrates of attention and awareness imply that they are the same processes? This is an important question for future research, about which we can only speculate. Some evidence suggests that it is possible to dissociate attention and awareness. For example, attentional priming has been shown to be possible in the blind hemifield of blindsight patients[78]. It might also be possible, however, to attribute these priming effects to the feedforward sweep. If this is the case, these effects should not be called attentional according to the above definition. A refined definition of attention and awareness might be required to bring

physiology and psychology into closer correspondence. The time might have arrived at which our understanding of the neural substrate has advanced sufficiently to guide this redefinition[79].

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