

## Coupling perception to action through incidental sensory consequences of motor behaviour

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**Abstract** | Researchers in the field of active perception study how sensory processes coalesce with motor actions to extract information from the world. Such actions intrinsically alter perceptual processing and have intended sensory outcomes, but also lead to incidental sensory consequences, which are side effects of moving the sensory surface to its intended goal. These incidental consequences of actions are generally considered a nuisance to perception that needs to be attenuated or suppressed during movement execution. In this Perspective, we propose instead that incidental sensory consequences of actions shape perceptual processes through action–perception couplings and we review evidence from the domain of active vision. We propose four hallmarks representing the degrees to which actions are an integral part of a perceptual processing architecture. Finally, we outline a research strategy for probing these hallmarks in active perceptual systems and conclude that researchers of perception should embrace the study of action kinematics in pursuit of their questions.

In journals, conferences, and departmental structures, research on how humans perceive is often separated from research on how humans move. Yet the tight link between perception and motor control has long been acknowledged<sup>1–6</sup>. Psychology and neuroscience have made remarkable progress in understanding the coordination of perception and action at the behavioural and neural level<sup>7–14</sup>, advancing understanding of how perception supports action<sup>6,15,16</sup> and how action supports perception<sup>17–21</sup>. Although the coordination of perceptual and motor processes has been substantiated, these processes are still considered fundamentally separable. Indeed, researchers across sensory modalities argue that perceptual processing needs to be sheltered from the sensory consequences of movement through attenuation or suppression during motor acts<sup>22–24</sup>. However, an alternative view is that to understand perception, researchers must embrace its coupling to motor control.

Visual perception provides a model for active perceptual systems in which actions and their sensory consequences are integral

components of the perceptual process. Actions including eye, head and body movements shift what information from the world lands on the retina<sup>4,25</sup>. The field of active vision — in part inspired by discoveries in the engineering of robotic vision<sup>26–32</sup> — investigates how visual processes coalesce with the control of motor actions. We refer to such actions as visual actions, as they are inextricably linked to a visual consequence: every movement of the eyes with respect to the world yields a corresponding movement of the world on the retina. Indeed, eye movements and perception interact in rich ways<sup>33,34</sup>. Much as perception in other sensory modalities is attenuated at the time of self-movement<sup>23,35</sup>, conscious visual perception is largely omitted while the eyes rapidly reorient to new locations. Ample effort has gone into understanding perceptual omission during saccades (rapid movements of the eye shifting gaze between locations), giving rise to numerous accounts of this phenomenon (BOX 1).

In this Perspective, we compile evidence that understanding perception requires consideration of its coupling to motor control.

We first present a taxonomy that distinguishes intrinsic, intended and incidental sensory consequences of actions. With a focus on active vision, we review evidence that incidental sensory consequences influence, provide input to and are used by the visual system. We next describe four hallmarks of active perceptual processing and argue that incidental sensory consequences of movements provide a versatile tool for investigating action–perception coupling — the degree of coupling of perceptual processes to actions. On the basis of this idea, we advance a research strategy that is suited to identify whether and how perception is shaped by motor action. We show how this framing of action–perception interactions informs future directions in perceptual psychology and beyond.

### Sensory consequences of actions

Perception serves movement control in many ways<sup>6</sup>. At the same time, motor behaviour structures perceptual input. For instance, the eyes alternate rapidly between slow movements that maintain a target in the fovea and fast movements that reorient gaze to a new target, keeping the retinal image in constant motion. We propose a taxonomy of the sensory consequences of self-movement based on their intentionality and the locus of their effects on perceptual processes: intrinsic consequences exert their effects through automated, internal processes accompanying movement preparation<sup>11,13,14,36</sup>; intended consequences modify the relation between the sensory system and the external world<sup>10</sup>; and incidental consequences are the unavoidable effects of moving the sensory surface itself (in vision, the retina)<sup>37–43</sup>.

These consequences are not entirely independent and can interact. For instance, during development, incidental sensory consequences are the beginning of intended movement outcomes as infants learn the utility of their actions<sup>44</sup>. Similarly, intrinsic consequences such as pre-saccadic attention shifts<sup>45</sup> or efference copy signals (copies of motor commands that inform perceptual processing)<sup>46</sup> might adapt to anticipate intended and incidental consequences of movements<sup>47</sup>. We briefly introduce intrinsic and intended consequences before focusing on incidental consequences.

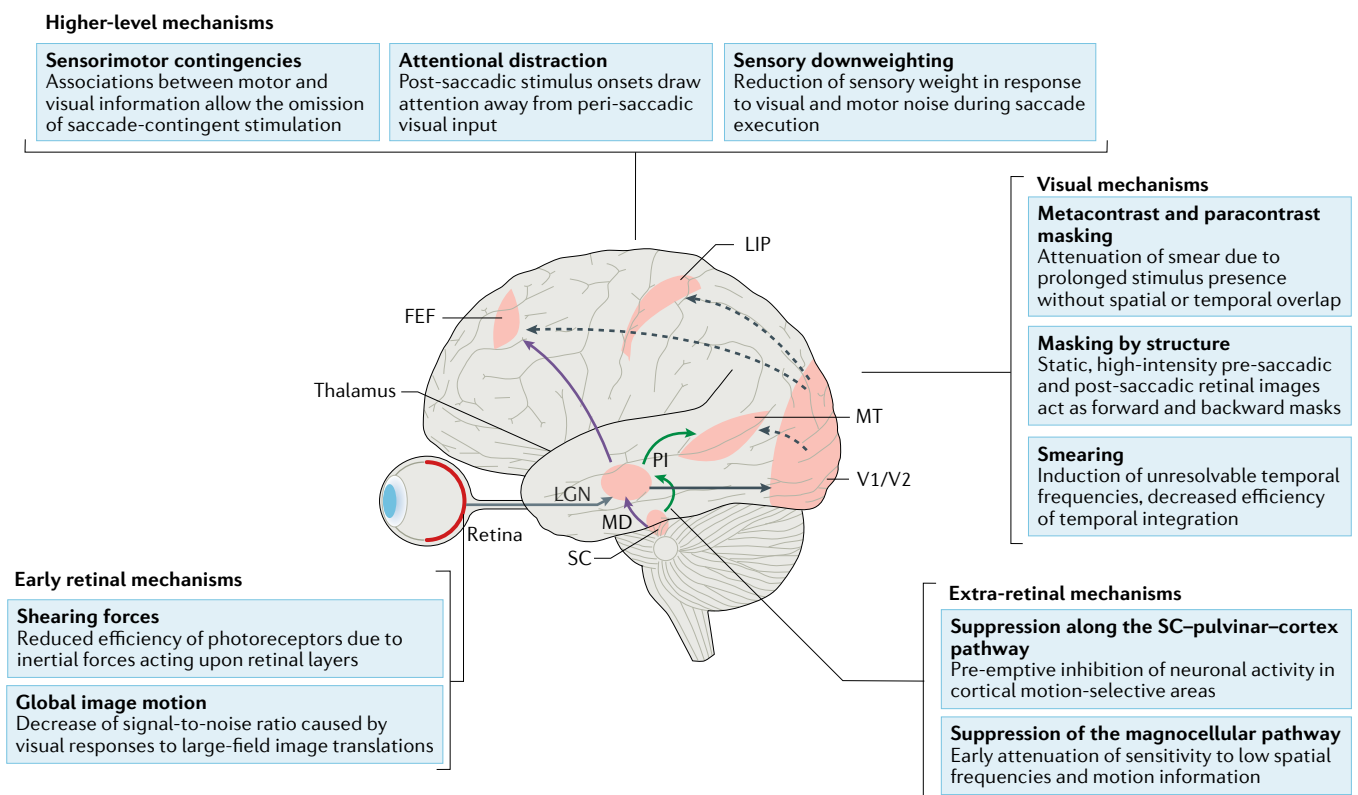
## Box 1 | Mechanisms of perceptual omission during rapid gaze shifts

Extensive research has identified mechanisms that contribute to saccadic omission at various stages of visual processing. In the retina, saccadic acceleration imposes shearing forces that mechanically bend the photoreceptors, reducing their luminous efficiency<sup>195</sup>. In retinal ganglion cells, translations of structured visual backgrounds cause transient activity that obscures responses to visual stimulation<sup>130</sup>. Structured backgrounds also reduce visual sensitivity, even when induced by rapid image motion during fixation<sup>126,128,129,196</sup> or by passive rotations of the eye<sup>197</sup>. The fact that contrast sensitivity during saccades is particularly reduced for low-spatial frequency stimuli<sup>198,199</sup> has sparked the idea that extra-retinal mechanisms suppress visual signals along the magnocellular pathway, possibly as early as in the lateral geniculate nucleus (LGN)<sup>200–203</sup> (see the figure). Corollary discharge from the superior colliculus (SC)<sup>50</sup> is relayed via the inferior pulvinar (PI) to cortical motion processing units in the middle temporal area<sup>13</sup>, where neural activity is downregulated during saccades<sup>204,205</sup>.

However, visual mechanisms have the most prominent role in saccadic omission of incidental sensory consequences. Saccadic velocities result in

extremely high temporal frequencies that are unresolvable by contrast and motion detectors<sup>41,198,206–208</sup>, and smearing reduces integration at any given retinotopic location<sup>209,210</sup>. Moreover, the presence of pre-saccadic and post-saccadic retinal images effectively masks intra-saccadic visual events<sup>38</sup>, even when saccadic consequences are simulated during fixation<sup>125,127,211</sup>. Notably, spatial or temporal overlap between stimulus and mask is not necessary — even distant post-saccadic masks<sup>95</sup> mitigate the perception of a smeared percept, resembling meta-contrast masking<sup>148,212</sup>.

Finally, high-level mechanisms such as the downweighting of incidental visual consequences due to motor or visual noise<sup>213</sup>, attentional distraction away from saccade-induced transients<sup>39</sup> or sensorimotor contingencies informed about the visual consequences of saccades<sup>103</sup> may contribute to saccadic omission. Whereas these accounts provide explanations for the omission of the incidental consequences of saccades, they leave open whether residual processing exists and serves a functional purpose.



FEF, frontal eye field; LIP, lateral intraparietal cortex; MD, medial dorsal nucleus; MT, middle temporal cortex; V1/V2, primary and secondary visual cortex.

**Intrinsic consequences.** Intrinsic consequences are changes in the internal state of a perceptual system that accompany a movement. For instance, the planning of visual actions within a scene (FIG. 1a) does not occur in isolation. Even before movement execution, motor preparation interacts with visual processes<sup>11–13,34,48–50</sup>. A key example is that the preparation of goal-directed movements influences attentional selection (FIG. 1b). The preparation of saccades leads to a shift of attention — a spatially confined improvement in perceptual discrimination

performance<sup>51–56</sup> observed at the saccade target and locations perceptually grouped with it<sup>57</sup> — resulting from increased sensory gain and tuning<sup>58–60</sup> as well as an increase in spatial resolution<sup>59,61,62</sup>. The pre-saccadic attention shift is thought to serve perceptual continuity across eye movements<sup>63,64</sup>, in part by encoding the saccade target into visual short-term memory<sup>65–69</sup>.

The effects of movements on visual processes also extend to visual information maintained in short-term memory<sup>14,70–73</sup>. Executing a saccade or a reach movement

to a location that contained a stimulus just a moment ago results in better memory for its features as compared with other locations<sup>74–79</sup>. This effect can be quite sophisticated. For instance, when a specific movement type renders a visual feature dimension relevant (for instance, object size is relevant to grasping), this movement-relevant feature dimension is preferentially stored in memory<sup>80</sup>. Intrinsic consequences of goal-directed movements therefore showcase integration between perception and action at multiple functional levels.

**Intended consequences.** Intended sensory consequences of actions are often the primary motivation to move; they change the spatial relation between the sensory surface (for example, the skin or the retina) and the external world. When exploring our environment visually, we manipulate objects with our hands to uncover their spatial structure<sup>19,81</sup> and move our eyes, heads and bodies to align our eyes with the part of the world that awaits exploration<sup>10,25</sup> (FIG. 1 c). Thus, intended sensory consequences of actions can be delineated into two categories — those that directly change the state of the world (distal), and those that bring the sensory apparatus into a new position (proximal).

Intended distal consequences result from a manipulation of the outside world by body movements. The intentional nature of these consequences presupposes that the person acting on the world intends to change it in some way. These consequences are thought to play a crucial part in development as children discover the effects of their actions on their environment. Indeed, even the visual detection of causal interactions in abstract events<sup>82–84</sup> and social interactions<sup>85,86</sup> might be shaped (over phylogenetic or ontogenetic timescales) by sensorimotor interactions with the world<sup>85–89</sup>.

Intended proximal consequences of movements change the position of the sensory system with respect to the world rather than the state of the world. Visual actions — from microsaccades that occur during visual fixation to large-scale eye movements that are often combined with head and body movements<sup>20,25,90,91</sup> — have proximal consequences because they change the position of the retina with

respect to the environment. For instance, walking around an object reveals parts of it that would otherwise be hidden from view. Similarly, a saccade that directs the photoreceptor-packed fovea to a particular object increases the clarity with which that object can be seen.

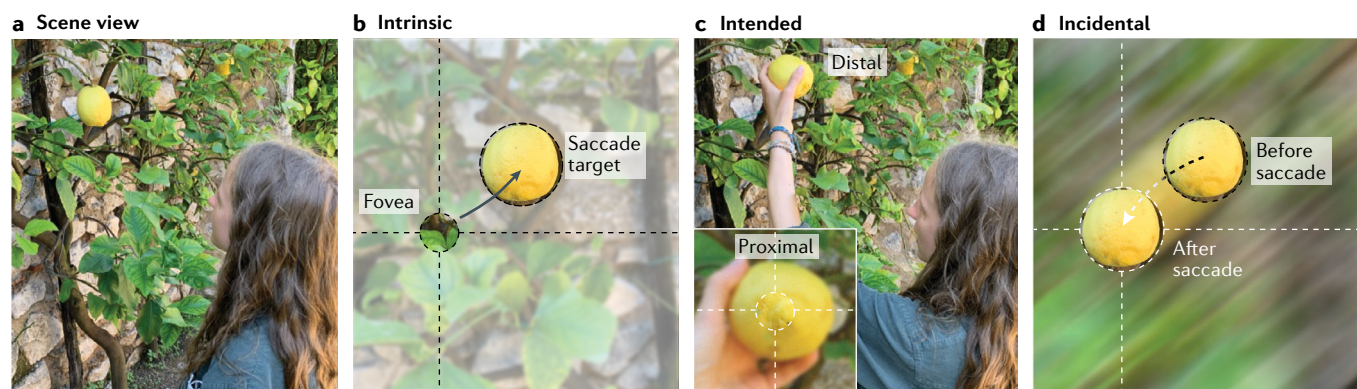
**Incidental consequences.** Beyond its intended outcome, each body movement also has incidental sensory consequences that result from moving the sensing body part to its goal. Consider reaching into your pocket for change: as you slip your hand in you pay attention to your fingertips<sup>36</sup> (an intrinsic consequence) until you touch the coins' surface (an intended consequence). At the same time, tactile sensors from your wrist and the back of your hand touch the fabric of your pocket, signalling upward motion. This tactile sensation is an incidental side effect of reaching the coins but carries unique and useful information about your movement (for example, how deep you have reached). In vision, looking back over your shoulder with a combined eye–head movement might be intended to bring the scene behind you into view, but executing this movement also results in massive incidental motion of the entire visual field across the retina (FIG. 1 d). Although this motion is not consciously perceived, it might still contain information about the magnitude and direction of the gaze shift<sup>92</sup>, as well as about the gist of the scene itself<sup>38</sup>. Research on incidental consequences of visual actions has almost exclusively focused on how the visual system counteracts (rather than exploits) them (BOX 1) — in spite of calls for a different approach<sup>2,93</sup>.

## Using incidental consequences

The fact that incidental sensory consequences of movements have been regarded as a nuisance to perceptual systems appears to be a symptom of a view in which perceptual processes need to be protected from harmful consequences of actions through cancellation, compensation, attenuation or suppression. However, we suggest that incidental consequences contain information that is unique and useful: the visual system might be able to use the incidental consequences of movements even if the movements ultimately serve a different goal. Several recent studies in the domain of active vision have started to build a case that studying incidental sensory consequences as a functional element of perception could enable a new understanding of the integration between motor action and vision.

The phenomenon of saccadic suppression describes a reduced sensitivity to low-contrast visual stimuli evident around the time of a saccade. This effect is often framed as a mechanism that eliminates visual input from further processing in an early and pre-emptive fashion. Yet this reduction in contrast sensitivity emerges during movement preparation, when sensitivity at the saccade target is actually enhanced<sup>53–56</sup>. That movement execution does not incapacitate vision was noted as early as 1962, when the effect of saccadic suppression was first reported<sup>94</sup>.

By contrast, saccadic omission describes a class of mechanisms that prevent incidental visual consequences from reaching conscious awareness even when reduced contrast sensitivity (saccadic suppression) would not affect them<sup>38,39,41,92,95</sup> (BOX 1).



**Fig. 1 | Three types of sensory consequence of visual actions.** When interacting with objects in a visual scene (a), visual actions have three types of sensory consequence: intrinsic consequences controlled by movement preparation, such as pre-saccadic attentional selection of a saccade or reach target (b); their intended visual consequence, such as moving an object (distal) or moving the body to place the fovea at a








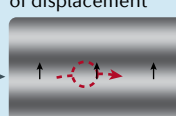
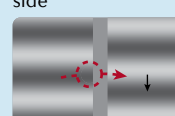
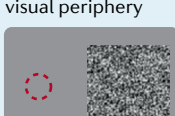
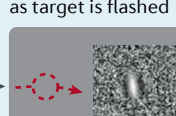

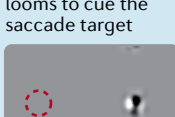
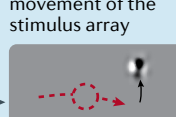
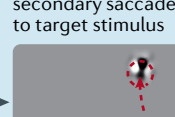
part of the scene that deserves closer inspection (proximal) (c); and incidental consequences of moving the sensory surface to its intended goal, such as intra-saccadic motion smear resulting from shifting a target into the fovea, and moving the scene from its pre-saccadic (black coordinates) to its post-saccadic (white coordinates) retinal position (d).


Indeed, even stimuli flashed around the time of saccade onset that are not consciously perceived can influence post-saccadic perception, to the extent that they contribute to a visual shape illusion<sup>92</sup> (FIG. 2a). This finding suggests that — despite saccadic suppression and omission that, on a conscious level, undoubtedly occur — incidental visual consequences of saccades must remain available to some extent on a subliminal level.

Regardless of suppression and omission, saccade-induced sensory consequences serve an important general function for post-saccadic vision: by moving the entire visual scene across the retina, saccades transfer the visual input from the spatial to

the temporal frequency domain<sup>43</sup>, producing transients that are crucial to visual functioning<sup>96–98</sup>. Given their high speeds, saccades modulate low spatial frequencies, enhancing contrast sensitivity in the early post-saccadic interval<sup>99</sup>. Indeed, if the onset of a low-spatial-frequency grating occurs during a saccade, sensitivity is increased compared with when the same stimulus is presented while the eye is at rest<sup>100</sup> (FIG. 2b). Consistent with this notion, low spatial frequencies remain resolvable at high velocities, whereas higher spatial frequencies do not<sup>41,101</sup>, and visual transients during saccades might facilitate post-saccadic processing of, first, coarse features and, then, finer details of a stimulus<sup>43,102</sup>.

Recent studies suggest that human observers might habituate to the incidental sensory consequences of saccades. After the repeated presentation of upward displacements of a large-field grating upon saccade onset (FIG. 2c), sensitivity to these displacements was reduced compared with sensitivity to displacements in other, non-habituated directions<sup>103</sup>. Importantly, this habituation was effective only when displacements occurred during saccades, suggesting that saccadic omission attunes to recent sensory consequences of saccades, or sensorimotor contingencies<sup>93</sup>. Thus, visual information that is not consciously accessible during a saccade is not discarded pre-emptively and could be exploited.

Study	Method	Key finding(s)
<b>a</b> Watson and Kregelberg (2009)	Line inducer flashed around participant's saccade onset  → Saccade executed to a predefined target location  → Elliptic probe stimulus assesses shape illusion  Inducer seen? Direction of elongation?	<ul style="list-style-type: none"> <li>• Peri-saccadic inducers were rarely consciously perceived (saccadic omission)</li> <li>• Inducers produced a post-saccadic shape illusion of the probe stimulus (circles appeared elongated perpendicular to the inducer's orientation), even when inducers were perceptually omitted</li> </ul>
<b>b</b> Boi et al. (2017)	Saccade cue defines a target location  → Transient condition: intra-saccadic onset of target stimulus    No-transient condition: post-saccadic onset with contrast ramp  Grating tilted left or right?	<ul style="list-style-type: none"> <li>• Contrast sensitivity improved when onsets of target stimuli occurred during saccades (transient condition) as compared with post-saccadic, contrast-ramped onsets (no-transient condition)</li> <li>• Improvement was present only for stimuli with low as compared with high spatial frequencies</li> </ul>
<b>c</b> Zimmermann (2020)	Saccade cue defines a target location  → Context trials: consistent direction of displacement  → Discrimination trials: displacement on one side  Left or right side displaced?	<ul style="list-style-type: none"> <li>• During discrimination trials, sensitivity to a displacement direction (up or down) was reduced if observers were habituated to the same direction during context trials</li> <li>• Habituation specifically affected displacements that occurred during saccades, whereas post-saccadic displacement remained unaffected</li> </ul>
<b>d</b> Scholes et al. (2021)	Dynamic noise presented in the visual periphery  → Spontaneous microsaccades occur as target is flashed  → Spontaneous microsaccades before/after target is flashed  Grating tilted left or right?	<ul style="list-style-type: none"> <li>• The reduction of visual sensitivity to grating orientation around microsaccades (saccadic suppression) diminished continuously over the course of seven daily test sessions</li> <li>• The decrease in suppression generalized to untrained orientations and retinal locations, but crucially depended on stimulus timing</li> </ul>
<b>e</b> Schweitzer and Rolfs (2021)	Peripheral stimulus looms to cue the saccade target  → Rapid intra-saccadic movement of the stimulus array  → Execution of secondary saccade to target stimulus  Target/latency of corrective saccade	<ul style="list-style-type: none"> <li>• Continuous intra-saccadic motion (as compared with equivalent apparent motion) led to an increased proportion of secondary, corrective saccades to the initial saccade target, and a reduction in their latency</li> <li>• Targets with orientations (incidentally) parallel to their retinal motion trajectory contributed more strongly to this effect</li> </ul>

Key: Gaze position/shift 

**Fig. 2 | Evidence that incidental sensory consequences may support visual and motor functions.** Description of methods and key findings from five studies that provide strong evidence for the notion that incidental sensory consequences are not simply eliminated from processing, but rather contribute to perception and action around saccades: Watson and Kregelberg<sup>92</sup> (a); Boi et al.<sup>100</sup> (b); Zimmermann<sup>103</sup> (c); Scholes et al.<sup>104</sup> (d); and Schweitzer and Rolfs<sup>112</sup> (e).



For example, saccadic suppression associated with microsaccades<sup>104</sup> is reduced when stimuli are presented predictably during saccade execution (FIG. 2d), suggesting that task demands might override saccadic suppression with training<sup>104</sup>. Suppression could also dissipate if saccade-induced sensory consequences (such as incidental retinal motion) are reliably absent, such that their dedicated suppression becomes irrelevant<sup>103</sup>. However, the exact extent of the interaction between suppression and processing of peri-saccadic information remains to be determined.

Incidental sensory consequences may hold valuable information that contributes to visual and motor functions. For instance, saccade-induced motion signals, and especially motion streaks<sup>105–111</sup>, could be processed as additional indicators of saccade amplitude, direction and velocity<sup>92</sup>. These motion signals are deterministically related to the ongoing eye movement and may be facilitated by natural scene statistics, which coincide with the statistics of saccades (BOX 2). Motion streaks might have a role in establishing object correspondence across saccades<sup>37,112</sup> because they could link the pre-saccadic and post-saccadic retinal positions of objects via spatiotemporal continuity<sup>69,113–115</sup>. This nascent idea has received strong empirical support: brief, continuous, ‘streaky’ object motion (as opposed to simple displacements), presented exclusively during saccades, facilitated post-saccadic gaze correction in both accuracy and speed, even when post-saccadic object features were rendered unavailable through masking (FIG. 2e). This facilitation was sensitive to the target’s motion direction, the features of the target and the distinctiveness of the motion streak in retinal coordinates, suggesting that unpredictable motion signals informed secondary saccades on a trial-to-trial basis<sup>112</sup>. Importantly, this result arose even though participants were unaware of the motion manipulation and exhibited barely above-chance performance when their task was to explicitly match pre-saccadic and post-saccadic objects on the basis of intra-saccadic motion streaks alone<sup>37</sup>.

Taken together, these studies suggest that how the incidental sensory consequences of saccades are omitted from conscious perception might be orthogonal to whether signals that undergo this filtering inform perception and action. These studies set the stage for a revised conceptualization of the link between perception and action, in which incidental sensory consequences of motor behaviour are an integral part

of perceptual processes and a continuous source of sensory information. On the basis of this understanding, we will explore next how visual actions can fundamentally shape perception.

### Action–perception coupling

We propose that actions shape the perceptual system as a consequence of the structured sensory consequences that they impose. Thus, perceptual processing carries specific signatures of the actions that influence it. The strength of this action–perception coupling increases (through learning) with the frequency at which the perceptual process is exposed to the sensory consequence of specific actions (FIG. 3a). Additional forces could affect this coupling; for instance, it should be stronger for stereotyped or predictable sensory consequences than for unpredictable ones. In the case of visual actions, the kinematics are highly stereotyped: across a large range of movement amplitudes, saccades follow a clear kinematic law in which the speed of the movement increases with the distance the eyes travel (the ‘main sequence’)<sup>116,117</sup>. Similarly, the kinematics of ocular drift during post-saccadic fixation exhibit reliable statistical properties<sup>118,119</sup>. Because these properties are directly replicated in the movements’ incidental sensory consequences, the coupling of vision to eye movements should increase over time as the consequences are repeatedly experienced.

Other forces might work against a high degree of action–perception coupling. One such force is the diversity of the spatiotemporal properties of external sensory stimulation. In vision, the coupling between perception and action should be maximal in static scenes or scenes in which action is adapted to the dynamics of the environment (for instance, optokinetic nystagmus that typically occurs while visually tracking a scene that is moving by quickly). In situations with low kinematic diversity of the external input, action kinematics are a reliable source of incidental sensory consequences. However, action–perception coupling should be weaker if the environment is, instead, highly dynamic and unpredictable (like in a busy train station), rendering the structure of incidental sensory consequences less reliable.

Another force pushing against a tight coupling of perception to action is the diversity of functional responsibilities of the perceptual system. For instance, a brain area that is involved in sensory processing may also serve additional functions (for example, visual perceptual areas are also involved

in visual memory or imagery<sup>120–122</sup>). Other functions may require different types of activity (for example, sustained rather than transient) or input (for example, top-down rather than bottom-up) from those that actions provide. In that case, lower coupling of sensory processing to the structure of sensory signals imposed by actions would make the brain area more versatile.

Interestingly, top-down influences on visual processing may also increase the action–perception coupling when they result from movement planning. These intrinsic consequences often originate in oculomotor control areas and are temporally linked to the onset of visual actions<sup>11–13</sup>. This temporal correlation might increase the effect of incidental sensory consequences on perceptual processing<sup>47</sup>. Indeed, in the extreme case that a perceptual system is needed for nothing but sensory processing, the degree of its coupling to visual actions would be maximal — only action-specific visual stimulation would cause perceptual processing, epitomizing a fully coupled, active visual system.

### Hallmarks of active perception

On the basis of these considerations, we define hallmarks of active perceptual systems that are diagnostic of the degree of action–perception coupling. Incidental sensory consequences of actions feature prominently for two main reasons. First, these consequences result directly from the integration of features of the environment with the kinematics of movement and cannot be understood by studying action or perception in isolation. Second, unlike intrinsic and intended sensory consequences, incidental consequences regularly remain outside conscious experience and therefore exclude strategic, cognitive influences. Focusing on visual actions, we propose a hierarchy of four hallmarks that indicate increasing degrees of action–perception coupling, exposing whether perceptual processing has access to, utilizes, is tuned to or even learns from incidental sensory consequences (FIG. 3b).

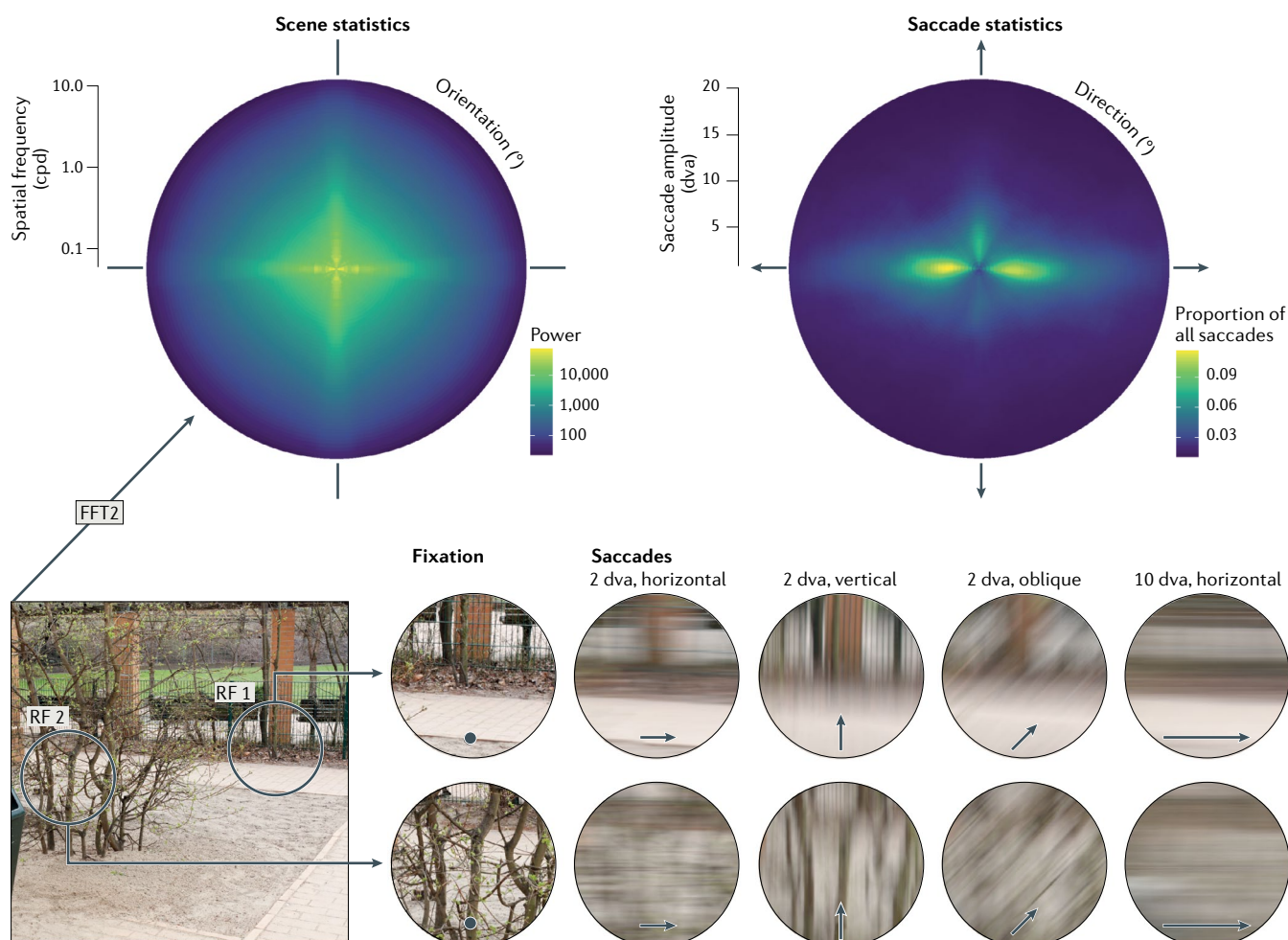
Hallmark I is that incidental sensory consequences of actions are not disregarded from, and do not disrupt, perceptual processing. Incidental consequences can be shown to remain available to the perceptual system even if they do not gain access to conscious awareness. For instance, there is strong evidence that intra-saccadic smear and motion can be perceived in principle, provided that they are not masked by pre-saccadic and post-saccadic images. Even in the absence of conscious awareness, such

## Box 2 | A curious link between the statistics of natural scenes and saccades

The properties of active visual behaviour during natural viewing resemble the image statistics available in natural scenes. Natural scenes exhibit logarithmic decreases in power at higher spatial frequencies<sup>214,215</sup> and higher power in cardinal orientations<sup>216,217</sup>. Saccadic eye movements have a similar preference for cardinal (over oblique) directions with an especially strong emphasis on the horizontal saccades<sup>91,118,218</sup>. It has been suggested that enhanced visual sensitivity to these orientations is related to, or even a consequence of, these statistical regularities<sup>219–222</sup>. To illustrate the similarities between scene and saccade statistics, we plotted the saccade amplitude and direction of more than 36,000 saccades from the Potsdam Search Corpus<sup>223</sup> as well as the spatial frequency and orientation content of the 130 stimulus scenes<sup>224</sup> (see the figure). The curious match between saccade and natural scene statistics enhances incidental

sensory consequences because these consequences are a combined function of both the statistics of the stimulus and the kinematics of the movement.

Using linear motion filters as a hypothetical model for visual input to receptive fields during rapid retinal image translations, such enhanced incidental sensory consequences can be appreciated visually: whereas orientations perpendicular to motion direction — especially at intermediate or high spatial frequencies — cannot be resolved at saccadic speeds<sup>41,101,210</sup>, parallel orientations give rise to motion streaks<sup>37,112</sup>, effectively coding high-speed motion as orientations<sup>105,106</sup>. Thus, the predominance of cardinal orientation in the visual system might also be a consequence of the fact that saccades along cardinal directions inevitably increase the power of parallel orientations in intra-saccadic visual input.



cpd, cycles per degree; dva, degrees of visual angle; FFT2, two-dimensional fast-Fourier transform, RF, receptive field. Image adapted with permission from REF.<sup>224</sup>, Johannes Mohr.

input can inform post-saccadic perception<sup>92</sup>, suggesting that it remains available for processing.

Hallmark II is that the perceptual system makes use of the incidental sensory consequences of actions. These consequences might serve a functional purpose in perception, cognition or motor control. There is a growing body of evidence that incidental consequences of saccades might indeed serve perceptual and motor

functions, such as enhancing post-saccadic contrast sensitivity<sup>100</sup>, regulating saccadic suppression<sup>103</sup> or facilitating gaze-correcting saccades<sup>112</sup>.

Hallmark III is that perceptual processes respond selectively to (are tuned to) the incidental sensory consequences of actions. As a consequence of this tuning, sensory events that reflect the kinematics of actions are sufficient (or even necessary, in the case of highly specific tuning) to initiate

perceptual processing. Kinematic signatures of actions should therefore be reflected in aspects of perception even in the absence of the action. For example, the visual system might treat visual stimulation that matches the input normally induced by saccades as a consequence of a saccade, even when no saccade has occurred. Saccade-like large-field motion might go largely unnoticed if its temporal or spatial profiles match those of the observer's saccades.

Indeed, a few studies have successfully used such simulated saccades to reproduce realistic motion smear<sup>37,123–125</sup> and replicate effects such as saccadic suppression<sup>126–130</sup> or the mislocalization of stimuli flashed around the time of saccades<sup>131–134</sup>. However, it remains unexplored exactly which kinematic properties of incidental consequences of saccades drive these effects.

Hallmark IV is that perception selectively learns from the incidental sensory consequences of actions and adapts to the relevant kinematics. The properties of perceptual processing therefore covary — across time, individuals and experimental or environmental conditions — with the properties of the sensory consequences of motor acts. Applied to the example of simulated saccadic motion above, Hallmark IV would be met if a reliable change in an individual's saccade kinematics — for instance, due to task demands, reward, disease or ageing<sup>135</sup> — was reflected in changes in their perception of high-speed motion.

### Evidence in active vision

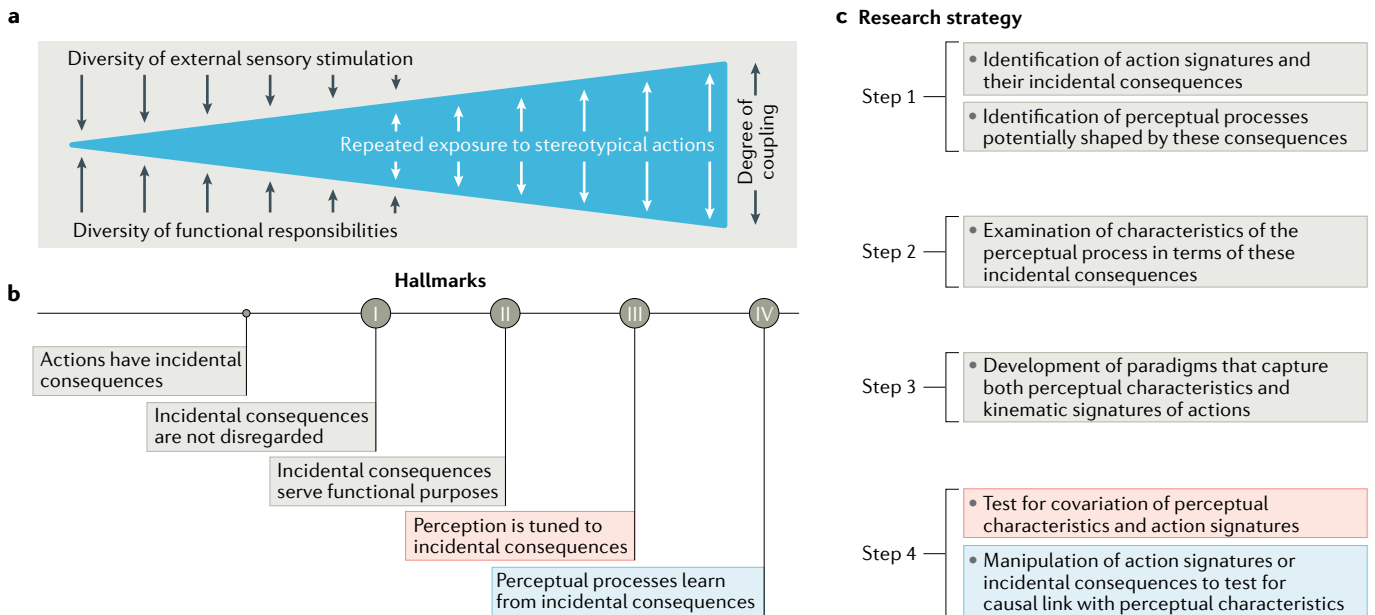
We have reviewed evidence that incidental sensory consequences of saccades influence active visual processing and are utilized for visual and motor functions (meeting Hallmarks I and II). Moreover, perceptual

functions are tuned to the incidental consequences of saccades (for example, the transients<sup>100</sup> or motion streaks<sup>37,112</sup> they impose) and such tuning is acquired through consistent sensorimotor contingencies in repeated actions<sup>103</sup> (for instance, consistent leftward shifts of text on the retina during rightward saccades in reading). On the basis of these results alone, it remains unclear whether such tuning — to a combined function of both the statistics of the stimulus and the kinematics of the movement (BOX 2) — persists in the absence of the corresponding action (Hallmarks III and IV).

Thus, visual processing in humans exhibits at least an intermediate level of coupling to visual actions. Explicit evidence for specific tuning of perceptual processes to the type of incidental consequences that visual actions impose (Hallmark III) or adaptation of the parameters of perceptual processes to the kinematics of visual actions (Hallmark IV) would be striking evidence that the consequences of actions permeate the visual processing architecture. A few studies, described below, provide hints at these deeper connections between features of perceptual processes and the kinematics of visual actions. These efforts have considered temporal, spatial or spatiotemporal aspects of visual processing.

**Temporal processing.** An early insight about active visual processing was that eye movements impose temporal structure on the visual input<sup>43,136</sup>. Through the retinal changes they cause, eye movements generate global visual transients, and therefore bursts of activity in visual cortex, across the entire visual field<sup>137,138</sup>. Following saccades, these transients are thought to drive synchronicity of neural responses across multiple visual areas<sup>139,140</sup>, influence visual sensitivity<sup>100</sup> and conscious perception<sup>141</sup>, and form part of a saccade-fixation cycle that initiates a coarse-to-fine processing sequence with the onset of each new fixation<sup>43,100</sup>.

Indeed, many aspects of visual processing occur on the same timescale as a saccade-fixation cycle (spanning a couple of hundred milliseconds) even though they are studied exclusively during fixation. These include the extraction of meaning from pictures<sup>142,143</sup>, the attentional blink (the transient inability to discover a second target in a rapid sequence of stimuli after discovering a first)<sup>144,145</sup> and attentional dwell time<sup>146,147</sup>, temporal masking (the perceptual extinction of a stimulus by a masking stimulus that is separated in time)<sup>40,148</sup>, various forms of postdiction, in which a stimulus alters perception of another stimulus presented earlier<sup>149,150</sup>, and other processes that occur on this timescale<sup>151</sup>. However, no systematic investigation has



**Fig. 3 | Framework of action–perception coupling and research strategy.** **a** | Provided two systems interface, they could show various degrees of coupling. Frequency of exposure of the perceptual system to stereotypical actions increases (white arrows) action–perception coupling. Other forces reduce action–perception coupling (black arrows), including the diversity of external visual stimulation (for example, the spatiotemporal structure of the environment) and the system's diversity of functional

responsibilities (beyond processing of visual input). **b** | Incidental consequences are a necessary but not sufficient requirement for coupling. Increased effects of incidental sensory consequences of motor actions indicate higher degrees of action–perception coupling, providing a hierarchy of hallmarks that are diagnostic of active perception. **c** | Research strategy to experimentally investigate potential, large degrees of coupling (Hallmarks III and IV).

yet directly linked these visual phenomena to temporal aspects of visual actions such as fixation durations, saccade latencies or other movement kinematics. For instance, it is unknown whether the duration of the attentional blink covaries with fixation durations across experimental conditions or environmental contexts, whether an individual's ability to extract meaning from rapid streams of images<sup>142</sup> relates to their saccade rate and whether individual differences in the duration of effective temporal masking are linked to the duration of an individual's saccades.

**Spatial processing.** The kinematic properties of visual actions might also contribute to spatial perception. Evidence for this potential link comes from trans-saccadic localization and the study of crowding<sup>152–155</sup>, a bustling domain of vision research that, with few exceptions<sup>156–160</sup>, studies peripheral vision exclusively during visual fixation.

Crowding describes the inability to identify visual stimuli in the periphery when they are embedded in clutter. The region around a target stimulus in which clutter leads to impaired identification is known as the crowding zone; this zone scales with the distance of a target stimulus from the fovea (eccentricity) and is elongated along the radial compared with the tangential axis (radial–tangential anisotropy). This crowding-zone shape resembles the scatter in saccades' landing positions (saccadic precision), which are also more variable in the saccade direction than orthogonal to it. Saccadic precision is related to observers' ability to detect displacements of the saccade target (experimentally induced during the eye movement). Target displacements parallel to the saccade direction are difficult to detect<sup>161</sup>, whereas orthogonal displacements are readily reported<sup>162</sup>. Moreover, an individual's scatter in landing positions along the radial and tangential axes of the saccade vector predicts their sensitivity to displacements in the corresponding directions<sup>163</sup>. This reflection of action kinematics in perceptual localization might have its origin in incidental sensory consequences of saccades — the spatial profile of uncertainty in localization could arise from the degree that the eyes repeatedly land off-target.

A direct comparison of variation in crowding, saccadic precision and spatial localization thresholds revealed a shared spatial profile across all of these domains<sup>164</sup>. Indeed, crowding zones and saccadic precision covaried across individuals even after correcting for shared influences of

eccentricity and the radial–tangential anisotropy. Crowding and saccadic precision are not inextricably linked at every time scale (for instance, on a trial-by-trial basis<sup>164</sup>), but their shared topology might still reveal a fundamental link to incidental sensory consequences of visual actions. In fact, computational modelling work has shown that intra-saccadic visual stimulation can confound image statistics in peripheral vision by way of learning processes in early visual processing<sup>165</sup>. Specifically, during saccade execution, saccade targets would stimulate the path between the target and the fovea, strengthening lateral connections in an attended zone around the saccade target. During fixation, these lateral connections would result in interference from flankers around a peripheral target. This putative mechanism predicts the exact shape of crowding zones: as saccades are directed towards peripheral objects, integration increases in the radial compared with the tangential axis, between the target and the fovea. Whereas some novel predictions of this mechanism were confirmed (for example, at eccentricities that saccades rarely target, crowding zones are more symmetrical)<sup>165</sup>, a direct link to saccade kinematics has yet to be established.

**Motion processing.** The most apparent incidental sensory consequence of visual actions is the motion they impose on the retinal image. There are interesting cases in which perceptual phenomena primarily attributed to saccades are reproduced during fixation simply by presenting retinal motion typically induced by saccades: saccadic suppression<sup>128,129</sup> and spatial mislocalization<sup>131–134</sup> around the onset of saccades were replicated in passive viewing conditions, suggesting that incidental sensory consequences impact visual processing around saccades. But motion is also relevant for the timing and coordination of actions to intercept a target and obstacle avoidance<sup>166</sup>. Motion processing should therefore be a prime target for investigating action signatures in perceptual processing.

Motion-induced position shifts provide an interesting study case for the interplay of saccades and perception. To intercept a moving stimulus, saccades need to target a location ahead of the object's current location, taking into account neural and motor delays between light hitting the retina and the fovea landing on the object. In addition, motion can drastically influence the perceived position of objects<sup>167</sup>. In the flash-grab paradigm, for instance, a brief stimulus is mislocalized on a moving

background that changes direction simultaneously when the stimulus is flashed<sup>168</sup>. This paradigm has revealed that humans might indeed see objects where our gaze would land on them rather than where they are: the magnitude of the perceived displacement that a person perceives during visual fixation is predicted by the movement latencies they show when executing a saccade to the same stimulus<sup>169</sup>. In this instance, visual motion processing is related to a kinematic property of saccades (their latency) even in the absence of a motor act.

Studies of motion perception have also shown that the visual system is particularly sensitive to biological motion, the kinematics of body movements of living organisms<sup>170</sup>. One particularly relevant finding is that human movements, including smooth pursuit eye movements<sup>171</sup>, exhibit the two-thirds power law<sup>172</sup>: the velocity of smooth pursuit movements is related to their curvature, such that velocity increases where the curvature is small and vice versa. Perception is tuned to motion that obeys this law even in the absence of motor acts: this type of motion is perceived as more uniform than motion at constant speed<sup>173–176</sup>, results in larger and more widespread neural responses in the visual cortex than other types of motion<sup>177</sup> and informs the anticipation of motion trajectories<sup>178,179</sup>. An intriguing possibility is that smooth pursuit contributes to biological motion tracking (an activity humans engage with daily). Owing to the direct coupling of eye movements to retinal motion, the visual system may learn from the incidental sensory consequences of pursuit, which replicate the kinematics of the pursuit target.

Thus, temporal, spatial and spatiotemporal aspects of visual processing all appear to reflect kinematic properties of visual actions. So far, the evidence in favour of this idea remains largely at a correlational level, but guides and provides fertile ground for future research.

### Uncovering action signatures

We propose a research strategy for identifying principles of perceptual processing on the basis of the effects of actions on the sensory input. Intentionally or not, the studies reviewed in the previous section pursued this strategy to some extent, uncovering hallmarks of the degree of action–perception coupling. Although the degree of coupling is an interesting research question in itself, probing these hallmarks strategically might put the investigation of this coupling in the service of understanding perception more broadly.



The proposed strategy consists of four steps (FIG. 3c). Starting from a given perceptual phenomenon, researchers first consider how actions could influence the process in question and find signatures of actions that the phenomenon might reflect. Properties of temporal masking, for instance, may reflect the duration of saccades and fixations, which vary across experimental or environmental conditions<sup>180</sup>. In the case of crowding, the spatial uncertainty associated with saccade targeting of peripheral objects varies as a function of saccade direction<sup>164</sup>. Finally, the perceived location of moving objects may relate to accurate saccade targeting<sup>169</sup>, which requires that motion prediction incorporates the saccadic latency between retinal input and oculomotor output and depends on properties of the moving target<sup>181</sup>.

The second step is to identify the characteristic properties of a visual phenomenon or function. Perception scientists have done this work for decades, but the search for properties should be guided by the action signatures identified in the first step. For the example of temporal masking, the relevant properties are the features, duration and location of the stimulus that can be masked, or the mask duration that is required to achieve invisibility. For crowding, the relevant properties are the spatial extent of the crowding zone for different eccentricities and directions, or the features of the clutter inducing the effect<sup>153–155</sup>. In the case of localizing a moving object, critical features might be the dependence on speed, location in the visual field or visual appearance<sup>167</sup>.

The third step is to find experimental tools (an experimental paradigm and appropriate stimuli) that are sensitive to the properties of the perceptual process and enable tracking of the action signature. For temporal masking and crowding, the paradigms that uncover their temporal or spatial features are well established. For the perception of moving objects, a revealing choice was to use stimuli that dissociate the objective from the perceived position<sup>169</sup>, as they allowed the isolation of perceptual and motor effects at the same time.

Finally, researchers should use the tools identified in step three to assess whether the perceptual phenomenon in question carries the action signature identified in step two. To ascertain the covariation, researchers can use the full repertoire of techniques available to behavioural science<sup>182</sup>: identifying correlations, enhancing or eliminating the action or its sensory consequences to investigate necessary and sufficient

conditions, or altering the kinematics of actions to uncover causal links to changes in perceptual processes.

For eye movements, these experimental techniques come with major methodological challenges. To mimic the natural continuity of visual input during rapid eye movements, stimulation techniques should have high frame rates, ideally without sacrificing spatial detail. Furthermore, when using gaze-contingent manipulations, even latencies of the technical set-up in the millisecond range<sup>183</sup> can introduce temporal and spatial mismatches between natural and experimentally induced visual stimulation. Replays of the visual consequences of recorded eye movements may suffer from measurement noise and need to consider ongoing eye movements. Finally, intrinsic and some incidental sensory consequences cannot be reproduced in the absence of eye movements (for instance, motion of screen borders). However, if implemented well, these manipulations can provide insights into the processing (Hallmark I), functional roles (Hallmark II), potential perceptual tuning to (Hallmark III) and learning from (Hallmark IV) incidental sensory consequences of movements.

When no covariation is evident between the properties of perception and the actions that influence it, there might not be a connection or the coupling might have a different origin than the one investigated. Notably, all studies that pursued the strategy we propose here have revealed aspects of the integration of perception and action, irrespective of the study outcome. At the moment, such studies are still a rare feat and we have focused on three examples from the existing literature. The approach put forth here — studying action to understand perception — can be applied to diverse phenomena and functions, and includes considerations of intrinsic and intended sensory consequences, enabling researchers to uncover deeper links between perception and action.

## Conclusion

Perception researchers have long considered incidental sensory consequences of motor acts a nuisance, a view that expresses a deeply rooted conceptual segregation of perception from action. In the domain of active vision, there is accumulating evidence that this segregation is unwarranted. We have identified four hallmarks of active perceptual systems that indicate that incidental sensory consequences might indeed shape visual processing. Supported by a systematic search for kinematic profiles of actions in

perception, these hallmarks are suited to guide research that will uncover fundamental properties of perceptual processing. The handful of studies that have (intentionally or not) pursued this strategy have revealed intriguing insights into temporal, spatial and spatiotemporal aspects of perception.

Thus far, the research on incidental sensory consequences of visual actions has put saccadic eye movements centre stage. However, visual actions at all spatial scales have incidental sensory consequences, including extrafoveal motion during smooth pursuit<sup>184</sup>, sudden offsets and onsets of the visual scene during eye blinks<sup>185,186</sup> and the incessant motion caused by fixational eye and head movements<sup>187–189</sup> as well as post-saccadic oscillations<sup>190</sup>. Every reliable kinematic property of these motor acts that translates into reliable incidental sensory consequences might leave permanent traces in perceptual processing<sup>187</sup>.

Our proposal gives rise to intriguing questions for future research. The arguments for action–perception coupling might also apply to other species<sup>191,192</sup>, sensory modalities<sup>23,24</sup> and types of behaviour<sup>7,136</sup>. Do non-visual sensory modalities use incidental consequences of motor acts (for instance, changes in the frequency spectrum of sounds during head movements<sup>193</sup>)? Questions also remain regarding how incidental sensory consequences relate to conscious perception: does a strong coupling of perception to action lead to a lack of awareness of the sensory consequences that actions impose?

Furthermore, how does structured input from other sources — such as dynamic environments, internal motor signals, other modalities or cognitive factors — structure perceptual processing? And how do intrinsic, intended and incidental sensory consequences of movements interact? Not all movement kinematics will be reflected in perceptual processes, and not every perceptual process is shaped by the sensory consequences of actions. Indeed, dissociations between perception and action can provide intriguing insights about visual and motor processing<sup>194</sup>, and could reveal forces that work against a close coupling between perception and action.

Studying action is key for understanding perception because action shapes perceptual processes through incidental consequences that act on the sensory surface. By providing an explicit research strategy to investigate this relationship, we hope that many questions regarding the action-based nature of perceptual processing will soon find more answers.

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