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Visual Perception: Tracking the Elusive Footprints of Awareness

Subjective visual experience leaves two distinct, overlapping ‘footprints’ within visual cortex: a small ‘footprint’ evident in multi-unit activity, and a much larger ‘footprint’ that dominates activity indexed by haemodynamic responses.

Randolph Blake[1] and Jochen Braun[2]

At a professional meeting in 1999 an overwhelmingly popular presentation was a poster manned by Yoram Bonneh from Israel’s Weizmann Institute. Throngs of people crowded around his video monitor to experience what can only be characterized as visual magic: a small cluster of stationary yellow dots disappeared from visual awareness for seconds at a time when those dots were surrounded by a swarm of coherently moving blue dots [1]. You can experience a version of this compelling phenomenon by navigating to: http://www.michaelbach.de/ot/mot_mib/ Dubbed ‘motion-induced blindness’, this beguiling visual illusion strikingly dissociates perception from reality and, thus, provides a powerful tool for identifying the neural concomitants of consciousness [2]. Three recent studies [3–5], employing closely related motion-induced blindness paradigms in monkeys and in humans, have now put this tool to excellent use to unearth results that appear neatly complementary and, for the most part, consistent.

All three studies contrasted neural responses associated with perceptual disappearance of a readily visible target surrounded by moving dots with responses associated with physical removal of that target. In two of these studies, the ones by Wilke *et al.* [3] and Maier *et al.* [4], macaque monkeys were trained to report their perceptual experiences while viewing a highly visible target presented to one eye together with a field of moving dots presented to the other eye or to both eyes; the moving dots surrounded but did not occlude the target. In the large majority of these trials, the animal reported that the target, although physically present, disappeared perceptually. Results from interleaved control trials on which the target remained visible or on which it disappeared physically confirmed the reliability and accuracy of the animal’s reports. In the third study, by Donner *et al.* [5], human observers viewed a clearly visible target while a cloud of dots rotated around (but never over) the target, thus causing the target intermittently to disappear from perception for several seconds at a time. Donner *et al.* [5] also included a replay condition in which the target was physically turned on and off in a temporal sequence mimicking the target’s perceptual fluctuations from a previous motion induced blindness trial.

In their monkey study, Wilke *et al.* [3] recorded target-evoked multi-unit activity and local-field potentials in visual areas V1, V2, and V4. They found that fluctuations in the perceptual presence of the target was reflected only in the multi-unit activity of area V4; in areas V1 and V2, neither multi-unit activity nor high frequency local-field potentials reflected the perceptual state reported by the monkey. Interestingly, however, the lower frequency bands of the local-field potential presented a completely different picture: here, the power of the target response, which was reduced by the onset of the moving dots, was reduced in all three areas (V1, V2 and V4), more so when the target disappeared from perception than when it remained visible. The latency of these perception-related reductions in the low frequency local-field potential components increased from V1 to V2 to V4, suggesting a feed-forward signal.

A tantalizing parallel to these results emerges in the recent study by Donner *et al.* [5], who used functional magnetic resonance imaging (fMRI) to measure blood oxygen level dependent (BOLD) signals in multiple visual cortical areas in the human brain. Evaluating the BOLD activity that accompanies perceptual target disappearance and reappearance during motion induced blindness, the authors focused on the retinotopic representation of the target in ventral visual areas V1, V2, V3 and V4. After discounting contaminations to the target response by attention (which is likely drawn to a perceptual transient) and by non-specific modulations (see below), the authors found that only within V4 did BOLD activity track the perceptual state of the target, dipping at or around the time the target perceptually disappeared and rising again when the target perceptually reappeared. The absence of perception-related BOLD modulations in areas V1, V2 and V3 stands in stark contrast to the significant BOLD modulations in these areas on the replay trials when the target was physically turned on and off.

In addition to this retinotopically localized modulation in BOLD responses, Donner *et al.* [5] also uncovered a second correlate of perceptual target disappearance, this one seen throughout the entire representation of the visual field including the target area, the area covered by moving dots, and the visual periphery. This 'global' response was delayed with respect to perceptual disappearance and was also present when the target was physically removed. Perhaps the global modulation accompanying target disappearance, whether physical or perceptual, is related to the surprisingly widespread activation that accompanies perceptual decisions in early visual areas [6].

So taken together, the studies by Wilke *et al.* [3] and Donner *et al.* [5] suggest that fluctuations of perceptual experience in the context of motion-induced blindness leave not one, but two overlapping 'footprints' in the activity of visual cortex: a small and retinotopically specific 'footprint' in higher visual areas, notably area V4, and a larger and retinotopically nonspecific 'footprint' at all levels of the visual hierarchy, beginning in area V1 (Figure 1). Interestingly, the salience of these two 'footprints' depends on the method used to assay cortical activity: the large footprint is barely noticeable in multi-unit recordings — its only trace being in the low-frequency local-field potential — but becomes readily evident in BOLD activity. Conversely, the small footprint is very evident in multi-unit recordings (both in multi-unit activity and in high-frequency-local-field potential), but is barely discernable in BOLD activity. In fact, only an exceptionally well-controlled experimental paradigm, such as that by Donner *et al.* [5], could hope to reliably identify the small footprint, as it is virtually swamped by the large footprint in the BOLD response.

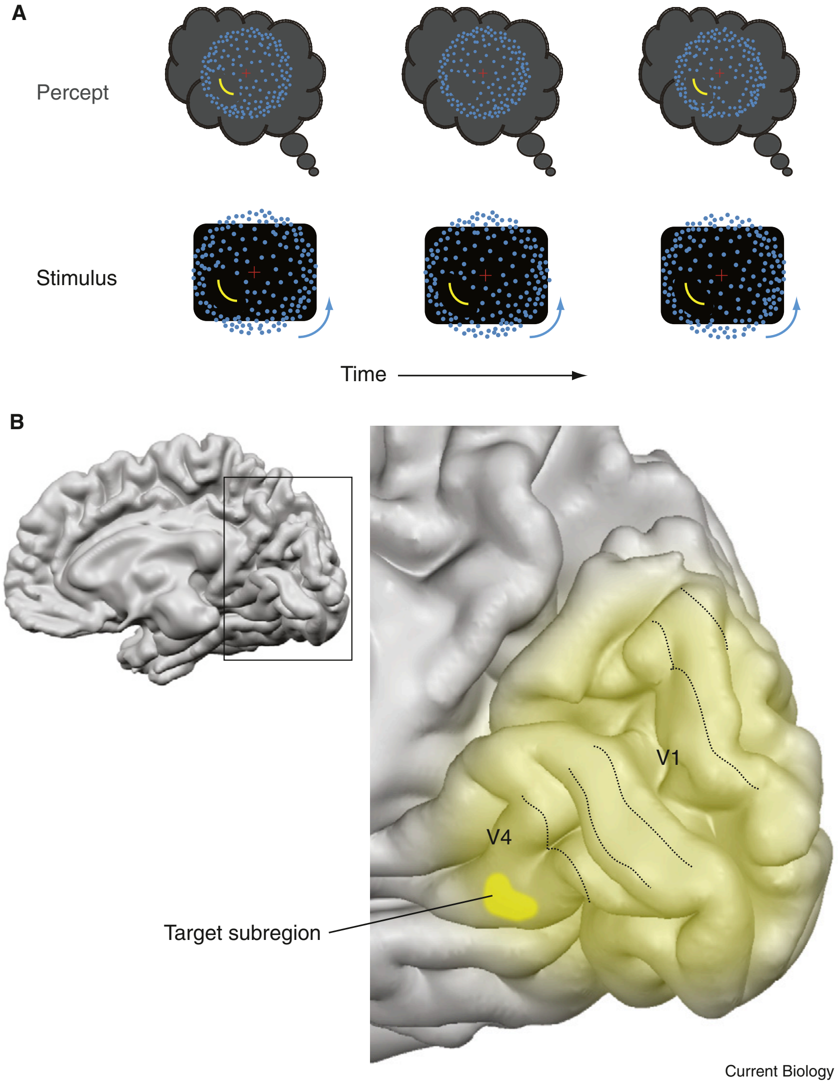

Figure 1. Neural footprints of motion-induced blindness.

(A) In motion-induced blindness, a clearly visible target (yellow arc) intermittently disappears from visual awareness when surrounded by a swarm of moving dots. (B) Two distinct, overlapping 'footprints' of this perceptual disappearance have now been identified in visual cortex. A small 'footprint' is readily evident in multi-unit recordings (spike rate and high-frequency local-field potential) in the target subregion of visual area V4 (intense yellow) [3]. A large 'footprint', covering the entire visual field representation in visual areas V1, V2, V3 and V4 (pale yellow), modulates the haemodynamic response [5]. A more refined analysis resolves this seeming inconsistency: a small 'footprint', which is restricted to area V4, is discernable also in the haemodynamic response. Similarly, multi-unit recordings show a subtle modulation of the low-frequency local-field-potential also in areas V1 and V2, at least within the retinotopic target representation [3,4]. It is still unclear whether this modulation also extends to other parts of the visual field, as does the large 'footprint' in the haemodynamic response. (We thank Tobias Donner for preparing the figure.)

The differential salience of the two neural concomitants of motion-induced blindness also shows up in work of Maier *et al.* [4], who compared single-unit recordings and BOLD activity measured in awake monkeys experiencing motion-induced blindness. Focusing on the retinotopic representation of the target in visual area V1, they found that the BOLD response tracked perceptual disappearance, whereas the spiking activity did not. Physical removal of the target, however, was evident in both BOLD and spiking responses. The only neurophysiological correlate of this large BOLD modulation in V1 was a subtle reduction in low-frequency local-field potential power.

But one question remains unanswered: is there correspondence between the motion-induced blindness-related BOLD modulations observed in human and in monkey area V1? Donner *et al.* [5] observed a global but no target-specific modulation (that is, activation stronger in target than in non-target voxels) in human V1, whereas Maier *et al.* [4], who did not compare target with non-target voxels, could not draw this distinction. Perhaps, then, the motion induced blindness-related BOLD modulations in monkey V1 are global in nature and, therefore, present within retinotopic regions of V1 well beyond the target representation.

So, thanks to the potent, intermittent perceptual suppression of vision induced by motion induced blindness, we are beginning to see how different components of neural responses within the visual hierarchy are related to fluctuations in visual perception, and we can expect to learn even more about the neural concomitants of motion induced blindness in the near future [7,8]. Moreover, we are beginning to witness some convergence between the results of monkey neurophysiology and human brain imaging in situations where perception and physical stimulation are dissociated.

It would be gratifying if the same convergence could be realized in the case of binocular rivalry, another compelling phenomenon in which visual awareness fluctuates even though physical stimulation remains invariant [2]. In the rivalry literature, there are nagging inconsistencies between human brain imaging results and monkey single-cell results, but no one has yet recorded single-unit activity, BOLD signals and local-field potentials during rivalry. Brain imaging studies of humans experiencing binocular rivalry reveal widespread, perception-related modulations of BOLD responses, including within the lateral geniculate nucleus, V1 and higher visual areas [9]. This distribution of brain regions differs from those exhibiting target-related BOLD modulations during motion-induced blindness, implying that the two phenomena are not mediated by the same neural circuits. However, the distinct circuits producing these two phenomena may embody equivalent neural operations that lead to equally compelling fluctuations in visual perception, in which case we could reasonably hope to see the same neural footprints associated with spiking, BOLD and local-field potentials for rivalry and motion induced blindness, albeit in different brain areas.

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Evolutionary Cooperation: Male Cleaner Fish Aggression May Promote Female Cooperation

A new study has shown that mixed-sex pairs of cleaner fish provide a better — more cooperative — service than singletons despite pairs facing an apparent Prisoner’s dilemma.

Maxwell N. Burton-Chellew

Why would Darwinian evolution produce organisms that act to increase the success of others? The evolution of such behaviour is problematic because, at first sight, cooperative behaviours appear to be disadvantageous, and yet cooperation is witnessed throughout Nature. The most powerful and successful explanation has been Hamilton’s theory of inclusive fitness [1,2], which explains how seemingly disadvantageous alleles can also increase their transmission *indirectly* by helping other individuals, typically close relatives, that are likely to share the same allele [1,2]. Yet cooperation also occurs between unrelated individuals and even between different species. The inherent instability of such cooperation between non-relatives is often conceptualised with the aid of the Prisoner’s dilemma [3] or the tragedy of the commons [4], whereby individuals do best by not cooperating (cheating), no matter what their partners do. This results in an inevitable outcome (hence ‘tragic’) in which all rational actors cheat, even though they all would be better off in the long-term if they had all cooperated, hence the dilemma [3,4].

A new study by Bshary *et al.* [5] has now shown that cooperation is achieved between individuals of a cleaner reef-fish species (*Labroides dimidiatus*) that service shared clients (Figure 1), primarily because females are more cooperative towards their clients when they are working with a male than when alone. This facultative cooperation may be a response to the threat of male aggression. The nature of this cooperation provides an added twist