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Vision as Motivation: Interhemispheric Oscillation Alters Perception.

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Introduction:

In preparing for this meeting, we were conscious of the heavy predominance of motor systems participants as opposed to those with a "more sensory" background. We therefore decided to present some work on the visual system that reverses the usual "bottom-up" approach and instead looks at a visual phenomenon that can only be understood in a "top-down" context. This reversal of thinking is becoming fashionable again, and you may be aware of continuing debates about whether the physiology of the primary visual cortex can explain aspects of visual perception or whether it is necessary to resort to "higher" levels of analysis. Even phenomena as basic as negative after-images, which are given as examples of retinal processes in text books, have recently been shown to have a high-level central component (Shimojo et al 2001). Hochstein and colleagues (e.g. Ahissar and Hochstein 1997) are also exponents of the emerging view that late visual processes may intuitively seem like an early processes (such as a brightness estimation, or the blinking of simple target on and off, as in the example we present below). Apparently more complex processes may be much earlier. The visual phenomenon we are going to present seems to be connected to the overall motivation of the subject, even though it concerns the simple appearance and disappearance of a bright target.

The phenomenon in question is Bonneh's illusion, which he and his colleagues call Motion-induced-blindness (Bonneh *et al.*, 2001). Three, stationary, bright yellow discs are presented against a swirling cloud of smaller blue dots. As bright and clear as the yellow discs are, they disappear and reappear in a quasi-regular but unpredictable cycle. This illusion was presented at the meeting and it can be viewed on the web at http://www.uq.edu.au/nuq/jack/rivalry.html or on Bonneh's site http://www.weizmann.ac.il/~masagi/MIB/mib.html. When it was first presented, some reacted angrily, claiming that Bonneh had switches under the table that he was using to turn off the yellow discs! Although there are a number of related illusions such as Troxler fading (Troxler, 1804) and the visual disappearance phenomenon reported by Ramachandran et al (1993), Bonneh and colleagues deserve some credit for taking this one to the point where all doubts can be eliminated over the possibility of its early origin. Because the disappearance of a yellow disc, in relation to its fellow discs, follows complex Gestalt rules of grouping, closure, good continuation etc, we know that it must be occurring at a high level of analysis where such forms of pattern recognition can take place, and not at early levels in the visual system. There are many experimental examples on Bonneh's website to illustrate the influence of Gestalt principles. Even a brief look at these makes it easy to convince oneself that this is a very high level phenomenon that "knows" a lot about image grouping and segmentation based on form and colour. We will give one example here:- If each disc is filled with parallel lines, its disappearance becomes subject to Gestalt rules of grouping by orientation; e.g. discs filled with lines of the same orientation disappear together, whereas discs oriented with their respective lines aligned in an orthogonal manner disappear independently. In other experiments one can show similar effects of grouping by colour or proximity.

In this paper, we are going to emphasise the message that the effect is taking place at a very high level by taking a further step. We show that the Bonneh illusion has all the hallmarks of perceptual rivalry (even though the rival alternatives are not obvious from inspection of the pattern before a disappearance takes place). In view of the raging controversy about whether binocular rivalry takes place in the primary visual cortex (V1) or much higher in the visual pathway, it might be argued that aligning the Bonneh illusion with the perceptual rivalries in general, does not constitute a compelling argument that Bonneh's illusion is "high." we will ignore this argument in view of the fact that V1 is already a relatively high level and, like perceptual rivalry, there is mounting evidence that Bonneh's illusion reflects interhemispheric oscillations (Pettigrew & Funk, 2001). Moreover, in keeping with the proposed interhemispheric involvement, the precise details of the illusion are influenced by two factors that show hemispheric interaction, an individual's mood (Baker *et al.*, 1997; Heller, 1993; Robinson, 1995) and personality (Caplan & Shechter, 1990; Sutton & Davidson, 1997). In particular, the proportion of time spent with one of the yellow discs disappeared is directly related both to the degree to which the observer has a positive mood and an impulsive nature, with euphoric and impulsive individuals reporting the highest proportion of time spent with a disc absent. In contrast, no disappearance at all was experienced by a highly stressed individual**.** This surprising finding emphasises the general point that apparently early visual processes may be influenced at the highest level. The result can be explained in terms of the growing evidence for hemispheric involvement in both rivalry and mood, given that the perceptual oscillations of Bonneh's illusion are a form of rivalry (Carter and Pettigrew 2002). We discuss this result in the light of the oscillatory nature of Bonneh's illusion, with particular emphasis on the possible role of neural oscillations in general.

Methods:

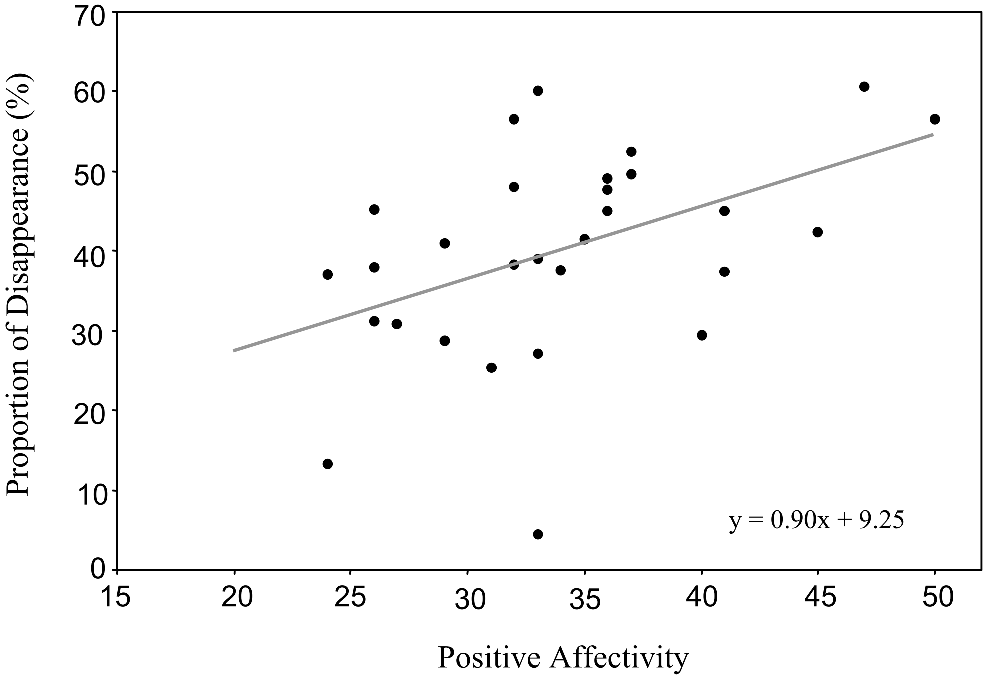
Twenty-nine subjects with normal or corrected to normal vision, were presented with Bonneh's illusion. They were unaware of the object of the experiment and were naïve with regard to the illusion itself. The illusion consisted of three stationary yellow dots and a fixation cross, overlaid on a global moving pattern of 150 blue dots set on a black background. The yellow dots subtended 0.5° of visual angle arranged along a 4° radius circle forming a triangular arrangement around a yellow fixation cross (0.5°) situated in the middle of the display. Subjects were instructed to fixate on the cross while attending to the yellow dots and report whether A) they could see all of the yellow dots in the display or B) if any of the dots had disappeared. Responses were indicated *via* key-press on a standard computer keyboard. Data was collected over a 10 minute period divided into 4x100 second trials, with a 30 second break between each trial. The display was presented to subjects on a standard Macintosh (iMac) computer monitor, in a dimly lit, quiet room and viewed from a distance of 60cm.

In order to assess an individuals mood state, we used a rating system developed by Watson and colleagues (1988), which has been shown to be a reliable, valid and efficient means of measuring positive affect (Watson *et al.*, 1988). Prior to the presentation of the MIB stimulus, each subject was asked to rate ten adjectives *(interested, distressed, excited, upset, strong, guilty, scared, hostile, enthusiastic* and *proud)* in relation to how they felt "right now, that is at this moment." The adjectives were rated from 1 to 5 where 1 = Very slight or not at all, 2 = A little, 3 = Moderately, 4 = Quite a bit and 5 = Very much. The ratings were then summed to give a score between 10 and 50.

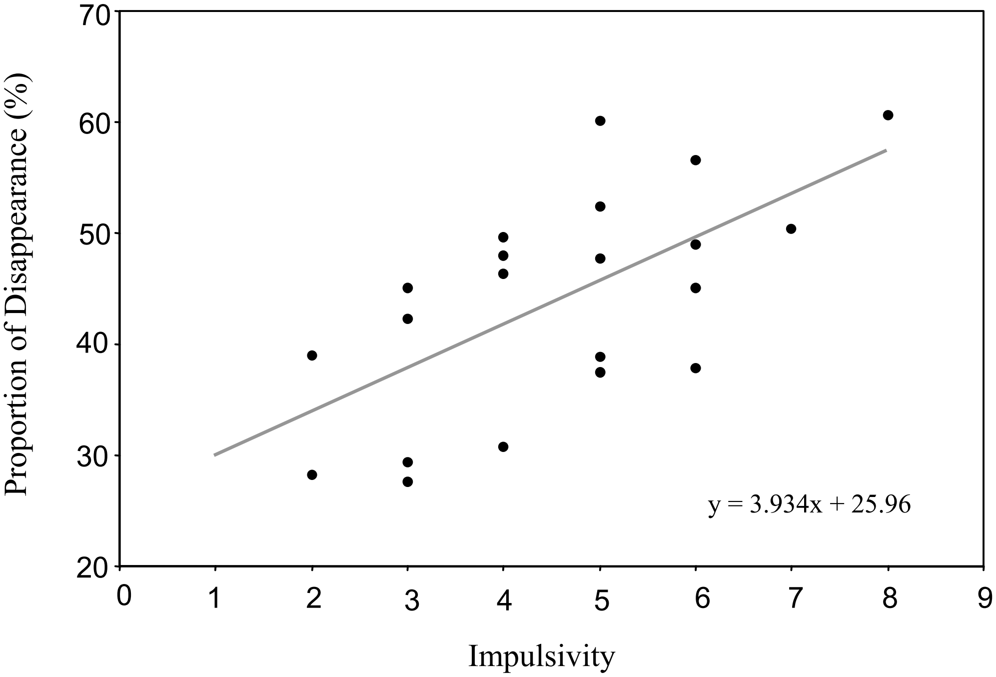
As a link has been shown between positive affect and impulsivity (Gray, 1987), twenty-one subjects were additionally administered the Eysenck impulsivity sub-scale (Eysenck, 1973). Subjects were asked to answer "Yes" or "No" to nine short questions such as "Do you often do things on the spur of the moment?" Each response corresponding to an impulsive tendency was given a score of 1, from which an overall impulsivity score out of 9 was calculated for each subject.

Results:

The proportion of disappearance experienced in Bonneh's illusion, calculated as the percentage of the total testing time, that any of the dots were reported to have disappeared, was found to increase with an increase in the subject's self-reported level of positive affectivity (R = 0.46). Through an analysis of variance, this effect was found to be significant ($F_{(1,27)}$=7.30, p =0.012). An even greater effect on the proportion of disappearance was observed with the degree to which the subject reported impulsive tendencies (R = 0.62). Again this effect was found to be significant ($F_{(1,19)}$=13.04, p



A)



B)

Figure 1. Proportion of disappearance induced by Bonneh's illusion in relation to A) positive affect measured by the PANAS (Watson *et al.*, 1988) and B) impulsivity measure by Eysenck's impulsivity sub-scale (Eysenck, 1973). Note the surprising correlation between these measures of mood and personality and the details of Bonneh's illusion experiences by each individual. A high index of impulsivity or positive affect is associated with a greater illusion, with the yellow discs disappearing for a greater proportion of time. This result is consistent with our hypothesis that the basis of this perceptual oscillation is an interhemispheric oscillation, with the left hemisphere responsible for the disappearance phase and hence for the longer disappearance phase in subjects with high positive affect and impulsivity, both of which are left hemisphere attribute*s*.

Discussion:
Bonneh's illusion is a perceptual oscillation that shares many similarities with more familiar perceptual rivalries such as binocular rivalry, the Necker cube, Shroeder's staircase etc. There is much debate about the origin of these rivalries and whether it is appropriate to place them under the same rubric (e.g. Andrews & Purves, 1997) or whether they represent completely independent phenomena with separate neural mechanisms and loci (Tong, 2001). We take the former view, arguing that the timing of

these oscillations at least share common elements that explain the remarkable coupling of the rhythms of different perceptual oscillations (Carter & Pettigrew, 2002). The current controversy surrounding the location and exact nature of the neuronal interactions responsible for perceptual rivalry is too extensive to be covered here, so the interested reader is referred to recent position papers on perceptual rivalries by Blake (2001), Tong (2001) and Pettigrew (2001). In this discussion we would like to focus on the remarkable fact that a basic visual event, the presence or absence of a yellow disc, is dependent upon the mood state and personality type of the observer! While mood and visual perception are intuitively unrelated, hemispheric asymmetries, like those implicated in perceptual rivalries (Miller *et al.*, 2000), have been associated with positive and negative mood states (Heller, 1993). Dominant activation of anterior regions of the left hemisphere have been linked to positive emotions (Baker *et al.*, 1997; Grisaru *et al.*, 1998; Robinson, 1995) while dominant activation of the right hemisphere appears to correspond to negative emotions (Martinot *et al.*, 1990; Pascual-Leone *et al.*, 1996; Soares & Mann, 1997). If one accepts that perceptual oscillations are linked to oscillations of the hemispheres, it is therefore possible to see that perception itself will be mood-related, an outcome that might be more familiar to artists than to vision scientists, but which is nevertheless robustly supported by the results we have presented. If we accept for the moment that perceptual oscillations can be linked to mood *via* interhemispheric oscillation (skeptical readers are referred to the position papers on rivalry cited above), then a burning question concerns the oscillations themselves. Why does perception oscillate?

Oscillations are a well-recognised feature of motor systems, if only because of the common locomotor requirement for rhythmic alternation of antagonists that is seen in both vertebrates and invertebrates. But antagonistic muscle action is not a satisfactory basis for the explanation of many neuronal oscillations. At this symposium a number of papers drew attention to oscillations in motoneuronal systems that were not easy to explain (Miles, Helsinki group). Even single cells oscillate, as in chemotaxis, where bacteria have a clock-like alternation (every 1.5 sec) between the opposite directions of rotation of the flagellar bundle that produce, respectively, forward motion (“go”) and tumbling (“stop”). In the case of the phenomenon that we have just described, interhemispheric oscillation, and its impact on mood and visual perception, the role of the oscillation is mysterious and generally elicits a strident “why?” along with the general discomfort that accompanies new, counterintuitive viewpoints. We would like to suggest that the oscillation in perception reflects high-level perceptual decision making. This would place visual perception closer to motor output than is generally recognized, but is consonant with emerging evidence that what may seem superficially like an early process is actually late (Ahissar and Hochstein 1997). Brightness estimations, for example, are usually thought of as “early vision” with explanations based in retinal terms, whereas the surprising new illusions of Dale Purves resurrect Helmholtz’ notion of “unconscious inference” where complex deductions precede apparently simple estimations such as that of brightness (Lotto & Purves, 1999; Williams *et al.*, 1998). The key problem emphasised by Purves is that visual inputs are inherently ambiguous and therefore require additional information to help resolve ambiguities, such as the relative contributions of the illuminant and the intrinsic brightness of the object. In the Bonneh illusion, we think that this additional information is provided by the coordinated activity of the two hemispheres. Each hemisphere adopts a different cognitive style, with regular oscillations between the hemispheres leading to alternations between the two styles. The pattern seeking left hemisphere, in one interpretation, rejects the stationary yellow disk on the basis of its discrepancy, a form of concrete "denial" in keeping with Ramachandran's (1994,1995) formulation of the cognitive style of the left hemisphere. An alternative view is based on the superiority of the left hemisphere in "form-from-motion" tasks that would emphasise the moving cloud of blue dots. Both these interpretations are quite compatible with each other and with the Purves thesis that global empirical information is brought to bear to make perceptual decisions in the face of ambiguity. Our addition to this thesis is that the coordinated activity of a whole hemisphere with a particular cognitive style could incorporate a number of related viewpoints of this kind and relay the sum to the decision-making apparatus. In the case of the right hemisphere, the style is veridical with discrepancies highlighted for investigation instead of being denied for the sake of a particular interpretation. An oscillation between right and left would ensure that neither of the complementary styles of the two hemispheres would prevail indefinitely. In this case one can see that the oscillation might also be connected to the resolution of the ambiguity (as in a variety of other areas that deal with ambiguity such as quantum physics and Taoist philosophy). Other explanations for the oscillation are possible.

We would therefore like to put forward for discussion a number of possible roles for neuronal oscillation. These are not mutually exclusive, as evolutionary stable strategies, of which oscillations are likely to be one, are often syndromes with many related features. Nor would we suggest that they are exhaustive, as we would welcome any further suggestions as to the role of oscillation. As a general principle, we think it important to keep in mind that current information about the encoding of timing within the nervous system is very sketchy compared with the information about the spatial location of different functions within the brain.

1. Coupled, Nested Clocks: Richard Feynman Thesis:

In the years before his untimely death, Richard Feynman was very concerned about how the brain represented time and visited JDP's lab at Caltech to discuss this problem. Feynman asked whether it was possible that the brain had a central clock that was responsible for ordering all processes in time, in the same way that modern computers have a central timekeeper. The answer to Feynman's question is still uncertain nearly thirty years later, but much more has been learned about neural clocks and pacemaker neurons, with intriguing evidence from flies, worms and humans that neural oscillators with vastly different scales, from milliseconds to hours, are coupled, in keeping with Feynman's notion of a master oscillator. According to this thesis, neural oscillations would be pervasive manifestations of timekeeping operations including perception and we would expect robustness and high heritability of the period for perceptual oscillation in an individual, as is observed

2. Adaptation to Ambiguity: Dale Purves Empirical Vision Thesis.

In an exciting new series of experiments that extends earlier work on visual illusions, Purves and his colleagues have elaborated a new thesis on the essential ambiguity of visual objects. It is impossible to decide, on the basis of the light emanating from an object, how much of this light is a function of the illuminant conditions and how much is a function of the intrinsic colour properties and reflectance of the object. Resolving the ambiguity must involve extra information apart from the patch of light reaching the retina from the object. This inescapable ambiguity requires that the brain resort to all sorts of empirical data on the probabilities of different illuminant and object conditions. Taking this thesis on ambiguity a step further, we propose that ambiguity may require that perception have an inbuilt oscillation, to avoid getting "stuck." This proposal is supported by new experiments that combine the Purves thesis about ambiguity with the prediction that they would be accompanied by perceptual oscillation (Carter and Pettigrew, unpublished). One important aspect of these perceptual oscillations is that one phase may be unconscious (e.g. the disappearance, or "denial" phase in the Bonneh illusion) and so they may not be obvious to inspection without special maneuvers to reveal their presence.

3. Phylogenetic Extension of a CPG Mechanism:

Rhythmic alternations between antagonistic muscle groups and opposite sides of the body are familiar to students of the motor system who are studying central pattern generators. Perhaps at high levels of processing in the CNS there is a duplication of these interhemispheric oscillators for increasingly more rostral (and therefore more metaphorical) functions. Alternation between complementary cognitive styles in the cerebral hemispheres may thus be a phylogenetic extension of earlier patterns of neural oscillation for opposing muscle groups.

4. Binding Mechanism: Wolf Singer Thesis.

Much has been written about this alternative thesis to explain the ubiquitous occurrence of oscillation in the nervous system. Dispersed neurons that are all part of a combined percept are thought to be linked (the "binding" phenomenon) by synchronous oscillations. This explanation for 40 Hz oscillations in the visual system has received some support from experiments on cats, monkeys, and even humans, but not from some monkey experiments where one would have expected it.

5. Improved Predictability and Precision of Timing: "Chorus Girl Problem."

When a line of chorus girls achieves perfect synchrony of their kicks, a feed-forward strategy involving internal oscillators is a more likely explanation than feedback from one chorus girl to another which would introduce small phase delays associated with latencies and reaction time. Instead of relying on moment-to-moment communication between chorus girls, each chorus girl could have a tunable internal oscillator whose phase and frequency could be set in relation to external cues. An array of oscillators, the line of chorus girls, could then be set up with perfect synchrony.

Conclusion:

The blatant perceptual oscillations of Bonneh's Illusion are somewhat unnerving considering our apparently stable view of the world. We think that the disturbing quality comes from the unique awareness that the illusion gives us into the inherently oscillatory nature of visual perception. This is in contrast to more classical examples of perceptual rivalry such as ambiguous figures where such oscillations can be easily rationalised away. The disappearance of bright targets also has a second feature that is interesting:- viz. It seems connected with a process akin to denial which eliminates component(s) of sensory information, if that component is discrepant with the individual's current belief system. If one accepts our interhemispheric interpretation for the moment, with the left hemisphere involved in a process like denial that ignores discrepant stimuli, one can see how visual perception can be influenced by seemingly irrelevant variables such as the mood or personality type of the observer. In this way our everyday experience of perceptual stability and objectivity may be even more illusory than the great mystics would have us believe. One phase of the perceptual oscillation, involving a denial-like process in the left hemisphere, that may be quite unconscious of the discrepancy with the other phase of the oscillation! Exploring this new view of perception should be an interesting pursuit.

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