William James prize article

Inner Vision: Seeing the Mind's Eye

Abstract

Does imagining a visual pattern involve the same mechanisms as actually seeing that pattern? If so, what are the functional consequences of this overlap? A new study shows that the simple act of imagining a visual pattern can change subsequent visual perception in a manner specific to the low-level perceptual mechanisms. This work is strong evidence that imagery involves mechanisms closely resembling those of normal visual perception.

Joel Pearson[*]
University of New South Wales
School of Psychology

Our ability to consciously experience the world around us has been dubbed one of the most amazing, yet enigmatic, processes under scientific investigation today (Koch, 2004). However, if we stop for a moment and think about it, our ability to imagine the world around us, in the absence of stimulation from that world, is perhaps even more amazing. To imagine the world gives us the ability to experience it as it is not, or as it might be in the future. This imaginative capacity, to experience objects or scenarios that do not necessarily exist in the real world, is perhaps one of the fundamental abilities that allows us to so successfully think about and plan future events. In a form of mental time travel, we can beam ourselves into the future and simulate an event, thus enabling us to imagine giving that talk in front of a huge audience or relaxing on holiday next week. Our possibly unique ability to imagine things that do not exist or are yet to take place, enables us to run a dress rehearsal of possible future events in our mind's eye.

For such a ubiquitous and important cognitive ability, little is known regarding the characteristics, mechanism(s), and limitations of mental imagery. There has been an ongoing debate regarding whether mental images are pictorial in a sensory manner like normal vision, or whether they are symbolic, without such sensory embodiment, more similar to cognitive thoughts (Kosslyn, Ganis, & Thompson, 2001; Pylyshyn, 2003; Slotnick, 2008; see figure 1).

[*] School of Psychology, The University of New South Wales, Sydney, NSW, Australia 2052. jpearson@unsw.edu.au
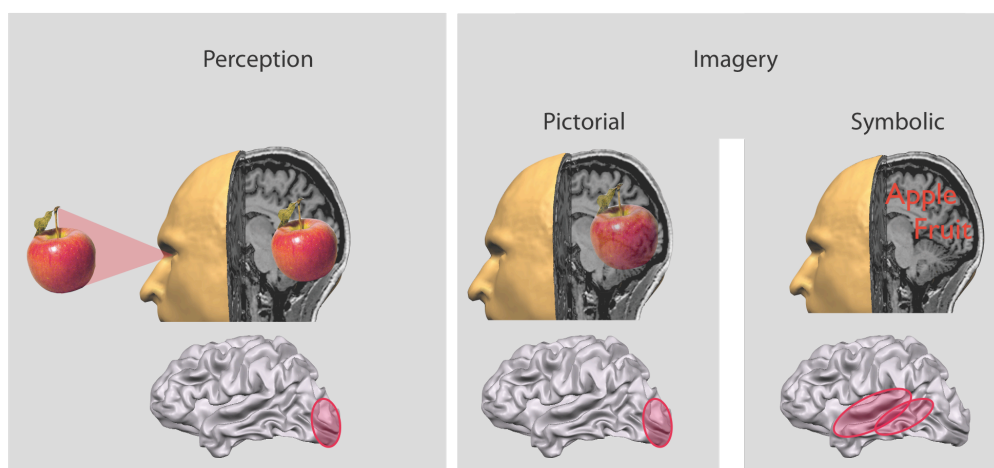
Figure 1. Visual imagery: pictorial or symbolic? What is it like to imagine an apple? Is the experience and corresponding neural processes pictorial, much like a weak version of visual perception or is the whole process more symbolic, like non-sensory thoughts or language?

There is a growing body of neuro-evidence that the act of forming a visual image in the mind's eye leads to neural activity in early visual areas such as V1 (Klein, et al., 2004; Kosslyn, Thompson, Kim, & Alpert, 1995; Slotnick, Thompson, & Kosslyn, 2005). These early visual areas are known to be retinotopic, in that they process visual information in a manner that preserves the spatial layout of the pattern of light hitting the retina of the eye. Hence, the spatial layout of neural activity in these early visual areas represents the spatial layout in the visual world. Imagery seems to involve activity in these areas; this suggests that imagery involves pictorial mechanisms similar to those of normal vision. If there is such an overlap in neural mechanisms between vision and mental imagery, then why aren't there more functional and behavioral consequences of such an overlap?

In a recent paper we demonstrated that visual mental images could have a strong influence on subsequent perception in a manner that suggests the content of imagery is represented in early visual areas (Pearson, Clifford, & Tong, 2008). These experiments used a visual phenomenon called binocular rivalry (Blake & Logothetis, 2002; Tong, Meng, & Blake, 2006). Binocular rivalry occurs when two dissimilar visual patterns are presented one to each eye, resulting in fluctuations of perceptual awareness between the two patterns. First an observer sees one pattern, then without warning, perception dynamically flips to the other pattern. These vacillations in perceptual awareness seem to continue in a largely unpredictable manner for as long as the subject views the stimuli.

In our experiments, we first had subjects imagine either one of the two binocular rivalry patterns. Shortly afterwards we would flash on both the rivalry patterns. The subjects would simply report which pattern was perceptually dominant. Surprisingly, we found that the pattern people had just been imagining tended to be dominant in the brief rivalry presentation: The content of what people were imagining was affecting dominance in subsequent binocular rivalry. If subjects imagined the red horizontal pattern, then that pattern had a tendency to become dominant during the next rivalry presentation. This basic finding struck us as important. It suggested that

the simple act of imagining a visual stimulus could subsequently change the way we see the world.

If imagery is processed in visual cortex in a similar manner to visual perception, then it follows that a perceptual stimulus might affect rivalry in the same way as imagery. We ran an experiment in which imagery was replaced with a perceptual stimulus: either one of the rivalry patterns. Here we were interested if, under some conditions, perception and imagery might display the same effects on the subsequent rivalry presentation. Indeed, we found that a weak perceptual stimulus (40% of the mean luminance of the rivalry patterns) tended to prime or facilitate dominance of that same pattern in the subsequent rivalry display: Both weak perception and imagery were having almost the same effect on subsequent perception. This suggests that imagery involves processes that could be akin to an attenuated version of normal vision.

Previous experiments have shown that visual attention can have an effect on rivalry dominance (Chong & Blake, 2006; Mitchell, Stoner, & Reynolds, 2004). Hence, we wondered what role, if any, attention might have in the current paradigm. We developed a stimulus to test the effects of attention on subsequent rivalry. We merged the two rivalry patterns together such that each was still clearly visible in a plaid-like pattern (see figure 2). This allowed participants to attend to either one of the elemental patterns in an otherwise analogous paradigm to the imagery and weak perception experiments described above.

Compound Attention stimulus
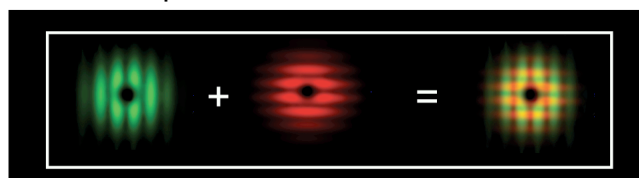
Figure 2. The stimulus used to investigate visual feature attention. By adding the two rivalry patterns we created a compound plaid stimulus. Subjects could attend to either elemental pattern (red or green) in the compound stimulus. This stimulus allowed us to compare feature attention with imagery and weak perception. Note that in the actual experiments we reduced the mean luminance of this compound stimulus.

In the initial experiments, we found that attending to one of the elements of the compound attention stimulus yielded results similar to those of imagery. When subjects attended to the green element of the attention stimulus, the green pattern tended to become dominant in the subsequent rivalry presentation. Hence, attention could prime rivalry in a manner similar to imagery and weak perception.

Next we investigated the time-course of imagery, attention, and weak perception. To do this, we compared the effects of imagery, attention, and weak perception when performed or viewed for different amounts of time (1-15 seconds). To control how long subjects performed imagery, we introduced a rapid serial visual presentation letter task directly after the allotted time for imagery. As this letter task was highly demanding, we predicted that subjects would have to cease performing the imagery task. This gave us a convenient method to control the length of active

imagery. Note that we kept this letter task in both the weak perception and attention conditions.

For both imagery and weak perception, short time periods (less than 5 seconds) resulted in only very modest effects on the subsequent rivalry stimulus. In fact, the effect of imagery and weak perception grew stronger monotonically with more time, with the strongest effects at 15 seconds. Attending to one element of the attention stimulus for only 1 second, however, was enough to strongly bias subsequent rivalry. In fact, unlike the effects of weak perception and imagery, attention did not significantly change with more allotted time. This suggests that visual feature attention and imagery can be dissociated, at least in terms of the temporal dynamics.

During pilot experiments, subjects reported that imagery somehow felt more difficult with an illuminant background. Hence, we decided to test the affect of background luminance on imagery and attention. Using the same attentional compound plaid-like stimulus, we ran both imagery and attention conditions with the background set to different luminance levels. The bias priming affects of imagery declined as a function of background luminance, whereas those of feature attention were almost unaffected by the different levels of background luminance. Hence, background luminance seems to affect imagery and attentional processes differentially.

While the content of feature based attention and imagery can have similar affects on subsequent conscious experience, the two mechanisms seem at least dissociable in terms of their time-course and susceptibility to background luminance. Within the current context at least, this dissociability suggests that imagery and feature attention might have different mechanisms.

If imagery really does rely on neural activity in early visual areas, then imagery should share some of the characteristics of these neurons. Orientation selectivity is a hallmark of early visual cortex (Fang, Murray, Kersten, & He, 2005; Hubel & Wiesel, 1968). Single neurons in early visual cortex often have a preferred orientation. Stimulation by this preferred orientation results in more neural activity than stimulation by other neighboring orientations. When this measure of activity is plotted as a function of the angle of stimulation, you get what is commonly referred to as an orientation tuning function, with the peak in the curve occurring at the neurons preferred orientation (Ling, Pearson, & Blake, 2009).

We wondered: If imagery is indeed processed by these orientation selective neurons in early visual cortex, then would imagery be orientation selective as well? We devised an experiment in which subjects always either imagined a vertical or horizontal pattern. On any single presentation the binocular rivalry patterns could be one of five different orientations, while always being perpendicular to each other. In this experiment, subjects were first presented with a cue for the imagery task, either of the letters *R* or *G*; the *R* informing subjects to imagine the red pattern and *G* informing subjects to imagine the green pattern. It is worth noting that the experimental design here is different from that in previous experiments. Here, because the imagery cues are randomized, the analysis could be done on a trial-by-trial basis, rather than depending on the level of perceptual stability that was the dependent measure in the previous experiments.

Imagery was indeed selective for orientation (see figure 3). The bias effects of imagery peaked when the rivalry patterns were vertical and horizontal (74% bias), the same orientation as those imagined. In other words, when the orientation in the mental image matched one of the rivalry patterns, imagery facilitated dominance of that pattern. When the rivalry patterns were rotated off vertical or horizontal by only 22.5 degrees, however, this effect declined. When the rivalry patterns were rotated 45 degrees, there was almost no facilitation from imagery.
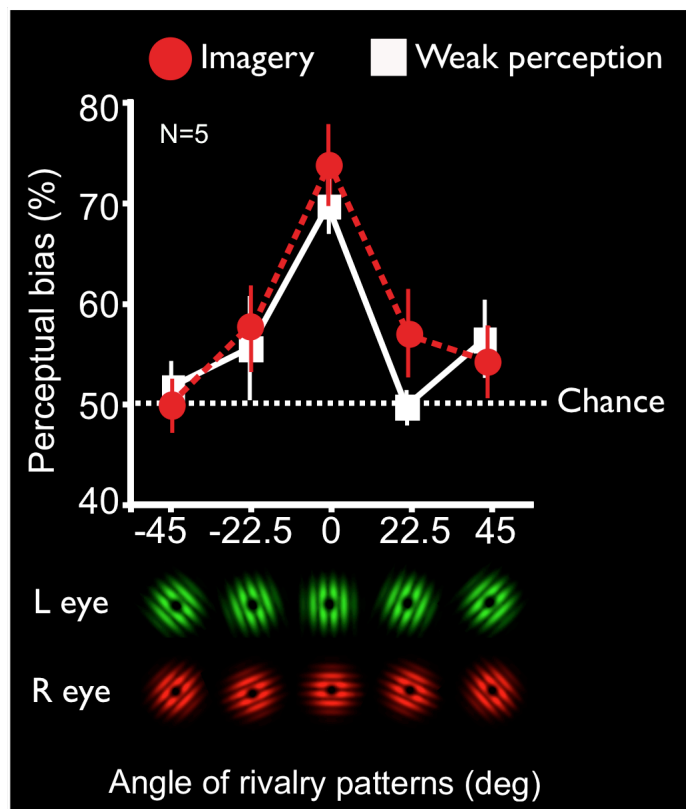

Figure 3. Imagery is orientation specific. Rivalry dominance was most strongly biased in favor of the previously seen (white) or imagined (red) pattern when the angle of imagery matched either orientation in the rivalry display. These data points form an orientation tuning function (*N*=5, data sorted for analysis by matching the color or imagery and rivalry dominance).

Besides providing evidence that imagery is orientation selective, this experiment suggests that these bias effects are not due to shifts in the observer's reporting criterion. There is no a priori reason why subjects should shift their binocular rivalry reporting criteria for different orientations. In other words, there is no clear reason why subjects would be more likely to report a particular rivalry pattern as dominant based on the orientation of the rivalry patterns. Hence, it is safe to conclude that the bias effects on binocular rivalry are due to the visual trace of imagery in early visual cortex, and not a binocular rivalry reporting criteria shift.

This result is strong evidence that imagery involves neural activity in early visual areas that is selective for orientation. We ran a further experiment to see if weak perception would bias subsequent rivalry in the same orientation selective manner. Indeed, a weak visual stimulus displayed similar feature selective effects on subsequent rivalry. This can be taken as further evidence of common mechanisms between imagery and weak perception.

Early visual areas are retinotopic in that they are organized in a manner that preserves the spatial layout of the light hitting the retina in the eye. This means, amongst other things, that two objects, spatially adjacent out in the world, will be represented by neighboring groups of neural activity in early levels of visual processing. We reasoned that if imagery is processed in early visual areas, then it too should display some form of retinotopic specificity. To investigate this issue, we devised an experiment in which subjects were required to always perform imagery in the lower right quadrant of visual space, while the subsequent rivalry display could appear, with equal probability, either at this location or in the upper left quadrant. In this experiment, subjects got the same randomized letter cue for imagery as previously described. Bias effects of imagery for the "same" location (lower right) were strong, as in previous experiments (see figure 4; left column). For the different location trials, however, there was no sign of any bias effects from imagery: The effects of imagery were local in visual space and they did not spread to the upper left quadrant. This result suggests that imagery, like perception, is processed locally in early visual cortex and is laid out retinotopically.
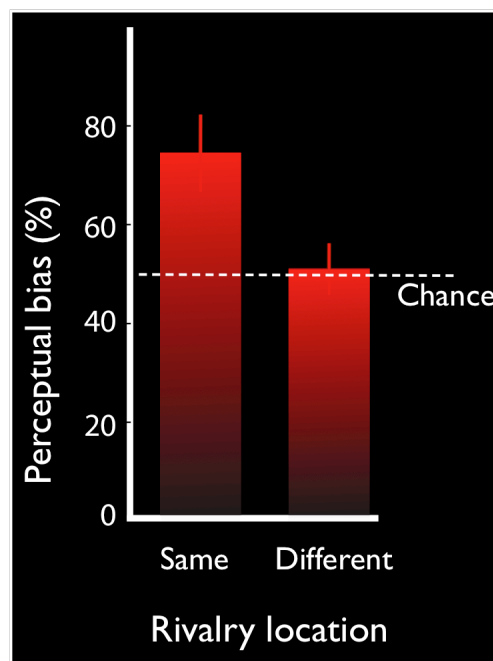
Figure 4. Location specific effects of imagery. For the same location in visual space imagery could bias subsequent rivalry. For a different location (diagonally opposite in the visual field), however, the dominant pattern in the rivalry display was unrelated to the content of imagery.

General Conclusions

This empirical work demonstrated that a single instance of visual imagery was enough to alter subsequent vision in a content specific manner. Surprisingly, imagery proved as effective as weak perception in biasing later vision. Visual feature attention can have a similar effect on subsequent rivalry, although its time-course and susceptibility to background luminance differ to those of imagery. The effects of both weak perception and imagery grew stronger with more time, and displayed local retinotopic, orientation selective bias effects on subsequent vision.

An interesting aspect of the discussed work is that these bias effects of imagery and weak perception did not have to be immediate. In fact, in some experiments, the act of imaging and the subsequent rivalry test were separated by five seconds of a challenging letter detection task. This suggests that once an image is formed in the mind's eye, that image leaves a lingering memory trace that can survive resource intensive behavioral tasks. This form of priming resembles a type of visual memory typical of intermittent bistable visual stimulation (Pearson & Brascamp, 2008). It is interesting to think that visual priming or visual memories can be formed in the absence of perception itself.

This work provides strong evidence that imagery involves pictorial mechanisms in early visual cortex (Slotnick, 2008). It has been argued that individuals performing imagery can create the mental image with any characteristics they please. The characteristics a subject will typically imbue to imagery are those of the physical or perceptual stimulus (Pylyshyn, 2003). Hence, if imagery resembles perceptual mechanisms, this is simply because the individuals performing imagery have engineered it that way. Simply viewing a visual stimulus, however, does not inform the viewer about the mechanistic dynamics of early visual feature processing (eg. orientation selectivity and retinotopic characteristics). Without a subject explicitly knowing the mechanistic characteristics of low-level vision, it becomes hard to argue that the similarities between imagery and vision observed in the current discussion are due to the subject's cognizant control over imagery formation. It follows then, that imagery inherently involves mechanisms that closely resemble early visual processes.

Imagery may present a valuable method for the brain to bridge high-level information (such as thoughts, memories, and learnt probabilities) with low-level sensory mechanisms. Imagery, like a form of mental time travel, enables us, or most of us, to simulate sensory events and objects, plan for future events, and make informed predictions regarding everyday decisions. We are only just beginning to understand this multifaceted critical cognitive ability and its far-reaching interplay with the full range of other cognitive processes.

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