
A test of the sensorimotor account of vision and visual perception?

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Abstract. Two theories define the relationship between sensory experience and perception of location. The doctrine of specific nerve energies relies on hard-wired, genetically specified relationships between stimulation and perception, modifiable only within limits by adaptation. In a newer sensorimotor account, experience tunes the relationship between stimulation and perception. The perception of pressure phosphenes can differentiate the two theories, because the phosphene appears at a location predicted by physiological optics and in a modality predicted by specific nerve energies. Moving a finger vertically along the outer orbit of the eye while pressing gently on it through the lid during nasally directed gaze results in apparent motion of the phosphene out of phase with the finger, therefore in contradiction to information from motor efference to the finger, tactile sense at the fingertip, eyelid and bulb, joint receptors, and proprioception from muscles driving the finger. A test of the sensorimotor theory giving it every advantage had six observers in darkness moving their fingers along the eye and observing phosphenes for 1 h and 2400 motion cycles; the phosphene always obeyed the doctrine of specific nerve energies, never adapting or changing modality as the sensorimotor theory predicts.

1 Introduction

How is visual perception calibrated to objects and events in the real world? This question, fundamental to all visual function, has a long history in psychology. Berkeley (1709) assumed that vision was calibrated by correspondence of visual input with touch, which he thought to be more reliable than vision, especially in the depth dimension. He had no empirical evidence, however, and it has turned out that, if anything, the touch/vision relationship is the other way around—it is easier to recalibrate touch from vision than vision from touch. Berkeley's efforts did leave a permanent legacy, however, in the recognition that there was a problem of intersensory calibration, and the insight that an active rather than a passive process would be required.

Successors to Berkeley's analysis were a number of hypotheses by 19th-century psychologists that form perception might depend on hand or eye movements, for instance visually fixating the vertices of a triangle to apprehend it. All such theories were demolished in a single step in some of the earliest psychophysical observations, in which even complex objects not noticed during direct exposure could be identified in afterimages (Helmholtz 1867, p.337). Further, even a single spark could briefly illuminate a scene and make its details visible. A variant of these theories depends on movements of the locus of attention rather than of the hand or eye, but the variant is both difficult to disprove and of little use in explaining the origins of perception.

The idea that crossmodal correspondence might be needed to calibrate visual input with the positions and motions of objects in the world remains, and has been studied extensively in the literature on prism adaptation (reviewed by Welch 1986). Because a prism resets the correspondence between visual and motor maps of the world, it disrupts the normal sensory–motor correspondence. Adaptation to the disruption is informative about the properties of the visuo–motor calibration; the calibration has turned out to be quite flexible, including the ability to adapt to two or more correspondences simultaneously in a few hundred trials (Welch et al 1993). Prism adaptation is a restricted

form of recalibration, however, limited to quantitative correction of corresponding angles in visual and motor systems. Significantly for the present theory, perceived visual position generally remains stable, while it is open-loop motor responses that change during adaptation.

The idea of defining sensory experience by motor feedback has persisted, however, finding its most recent expression in a sensorimotor theory of O'Regan and Noë (2001). According to these authors, the experience of seeing, for example, can occur only when the organism masters the laws of sensorimotor contingency. Vision is characterized by changes in input that correlate with eye and head movements, while audition is defined by being subject to change by head but not eye movements. Eye movements along a straight line result in no change in the retinal elements stimulated by the line, while movements along curved lines change the elements stimulated. According to O'Regan and Noë, the laws of sensorimotor contingency constitute the way the brain codes visual attributes. The point of the theory is not just that the contingencies affect perception; they actually define the nature of perception itself. Visual perception requires sensorimotor contingencies, based on action.

This theory is in contrast to the doctrine of specific nerve energies, first developed by Johannes Müller. Helmholtz (1867) attributes the idea to Müller and describes it clearly: “by stimulation of single excitable nerve fibers only such sensations can occur, that belong to the qualities of a single specific sense, and every stimulus that is capable of exciting these nerve fibers calls forth only sensations in this sense” (p.193, translation by BB). Helmholtz goes on to cite examples such as mechanical stimulation of the eye, which gives rise to visual rather than tactile sensations. According to this idea, the organization of perception is based on hard-wired connections that are committed to a particular sense independent of the pattern of the excitation that they carry. A corollary of this concept, pointed out by Helmholtz, is that projections are also committed. Up on the retina is down in the world because of physiological optics and hard-wired connections from the retina to the cortex.

The results of mechanical stimulation of the eye were suggested as a disproof of O'Regan and Noë's theory (Bridgeman 2004). The demonstration is a simple one that anyone can repeat—one simply looks nasally, and presses gently on the outer canthus of the eye just in front of the bony orbit, where the upper and lower lids meet. A pressure phosphene will appear on the nasal side of the visual field, usually as a circular dark patch with a bright rim, superimposed on the side of the nasion, the patch of skin between the forehead and the bony ridge of the nose.

Pressure phosphenes were first reported in Western literature by Alcmaeon of Croton in the 5th century BC, but were misinterpreted by Greek philosophers as evidence of light emanating from the eye. The interpretation of the phosphene as caused by deformation of the retina was first proposed by Johannes Kepler (reviewed by Grüsser and Hagner 1990).

The properties of the phosphene seem to violate what O'Regan and Noë would predict; it appears on the side of the visual field opposite the finger, in agreement with physiological optics but in contradiction to the position of the tactile stimulation. Moving the finger up (against the gravity vector with upright head) makes the phosphene move down (with the gravity vector), and vice versa. In this demonstration, multiple sources of information about the phosphene's position contradict its actual appearance: information from motor efference to the finger, tactile sense at the fingertip, eyelid and bulb, joint receptors, and proprioception of muscles driving the finger all signal an event on the outer canthus, but the phosphene is seen in the medial field, with motions opposite those signalled by the redundant non-visual sources. The phosphene remains the odd man out, not coming into correspondence with the other stimuli.

One could argue, however, that the pressure phosphene is not a fair test of O'Regan and Noë's theory. The phosphene contradicts a lifetime of visual experience, and is experienced simultaneously with visual objects that appear in their correct locations. To ameliorate these objections, and give O'Regan and Noë's theory every chance to be vindicated, we performed a phosphene experiment in which the brain was given an extended opportunity to sort out the contradictory appearance of the phosphene, with consistent exposure but without other retinal information.

2 Method

2.1 Observers

There were six volunteer observers, four male and two female—the author, one graduate student, and four undergraduates. The students knew that the experiment was about motion of pressure phosphenes and how they might change with practice, but were not aware of the competing hypotheses. For each observer, before the current experiment, total cumulative lifetime exposure to pressure phosphenes was a few seconds.

2.2 Procedure

All observers were first briefed on how to elicit a pressure phosphene through the eyelid and make it move, using their own forefinger on the outer canthus of an eye that is deviated nasalward, away from the finger. They were also told that any result, no matter in what direction, would be interesting and significant. For the experiment they then sat in darkness in a light-tight room, with black walls and ceiling, for a period of 1 h of alternating phosphene elicitation.

Prompted by the senior observer, an epoch of phosphene motion began when each observer moved the finger across the outer canthus of the eye through 1 up-and-down cycle s^{-1} for 60 s. The prompter called out the first few cycles, and then every 10 cycles from 10 through 60. After a half-minute rest period, a second phosphene epoch began with the same procedure as the first. Following another rest period and a third 60 s phosphene epoch, all observers closed their eyes and the room lights were turned on for 10 s to light-adapt the retinas during the half-minute rest period. All observers then switched to their other eye, to avoid irritation of the eyebulb, eliciting phosphene motion as outlined above for 3 more epochs of 60 motion cycles and one rest period each.

The sequence was repeated, with a light exposure and switch of eyes after every 3 epochs, for 1 h, resulting in 40 epochs of phosphene motion exposure 20 in each eye, for a total of 2400 motion cycles without contradictory information from normal vision of external objects.

Immediately after the 1 h exposure period, the observers individually reported their perceptions of motion and any other effects.

3 Results

All six observers could find the phosphene in each eye without difficulty, and could identify the direction of motion of the phosphene that corresponded to finger motion. All experienced an initial phosphene location nasally, opposite the finger, and saw vertical motion in the direction opposite the finger motion.

Exposure to the room lights through the eyelids during the experimental period resulted in a full field of bright red–yellow sensation during the exposure, and a bluish afterimage for a few seconds afterward. The afterimage disappeared before the next phosphene-motion cycles began.

In each observer, the appearance of the phosphene consistently obeyed the prediction of the doctrine of specific nerve energies, and contradicted O'Regan and Noë's sensorimotor theory. Its position and motion remained opposite the finger, and it remained visual rather than tactile. So the score is Johannes Müller 6, O'Regan and Noë 0.

4 Discussion

One might object that the experiment was not a fair test of the sensorimotor recalibration theory, though we made every effort to optimize conditions for its predictions to be borne out. We used an extensive observation period, required active motor behavior rather than passive observation, eliminated contradictory sensory information, and obtained unanimity from several observers. Still, a 1 h exposure period with 2400 motion cycles might not be enough to overcome previous experience.

This argument could be leveled against any duration of experiment, of course, short of a lifetime. Evidence that our exposure period should be adequate for sensorimotor recalibration comes from a large literature on adaptation experiments, where motor adaptation to prisms normally takes place in much less than 1 h and less than 2400 trials (Welch 1986). Adaptation of the vestibulo-ocular reflex also takes place in less time and fewer trials than our exposure condition (Welch et al 1998). If adaptation were to take place, it should take place within these limits.

A stronger interpretation of the sensorimotor theory, however, predicts that the phosphene should not be experienced as a visual phenomenon at all. Before the experiment, our observers had minimal experience with pressure phosphenes. The sensations they experienced during the experiment were correlated with mechanical actions of the finger, unlike visual sensations, and therefore according to the theory should have been experienced as tactile. Further, the phosphenes did not disappear with eye blinks or eye closures, further indications that they should not be perceived as visual. The brain should have been able to use its redundant information sources to correctly identify the phosphene as a tactile source rather than a visual one. This never occurred in any of our observers.

In conclusion, it seems clear that the O'Regan and Noë theory, while thought-provoking, does not stand up to empirical test. Modalities of sensory experience and interactions between stimulus motion and experience follow physiological rules built into the nervous system.

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