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Color in action: how the visual system uses color to guide movements

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I. Introduction

There are infinite ways to describe how it feels to fall in love. Sometimes, it is expressed as beginning to see the world in color.

Color is a fundamental aspect of human perception. Despite the metaphors, we are born with the ability to perceive color, although such ability is not fully developed until at least three months of age (Teller, 1998).

Colors are present in nearly every dimension of our lives, our perception of natural environments, our cultural and artistic expression and our ability to interpret and interact with the world.

Artists skilfully employ color to reproduce what their eyes see or instead depart from realism by using color in a certain way to evoke and convey an emotional response.

Color is deeply embedded in culture, language, art and emotional expression. We often associate a particular color with an emotion and use it to communicate, i.e., “Seeing red” or “feeling blue”.

Their cultural significance can vary across different societies: for example, red is often associated with danger or passion in Western cultures, while in China it represents luck and prosperity.

Furthermore, across different cultures, color categories and naming conventions vary widely (Berlin & Kay, 1991), although some studies suggest the existence of a form of universality in color naming, true for mostly industrialized societies (Kay & Regier, 2003).

From an evolutionary perspective, color vision emerged as an adaptive advantage that supported survival. For primates, this advantage could represent, for example, the ability of distinguish ripe from unripe fruits (John D Mollon, 1991; Regan et al., 2001).

It’s been shown that color plays a fundamental role in improving not only the recognition of a scene, but also how well we are able to memorize and recall its details (Gegenfurtner & Rieger, 2000; Wichmann et al., 2002).

In everyday perception, color plays a fundamental role in how we interpret form, depth and material properties. When viewing a scene, color information is necessary to segment different elements such as the objects from their backgrounds and to infer lighting conditions (Land & McCann, 1971) or surface reflectance (Brainard & Maloney, 2011). Color perception is a

highly adaptive and context-dependent process that interacts with behaviour, attention and motor planning.

Color is a subject of interest across multiple disciplines, from perception science, to physics, to the arts, and the research in this area reflects the diverse backgrounds of those who contribute to it. In the next section, I will introduce the major contributions to the modern history of color science.

Scientific history of color vision

Color vision has fascinated scholars since Aristotle's *De Anima*. Modern color science begins around the 17th century. Isaac Newton's prism experiments, which he called *Experimentum Crucis*, fundamentally transformed the understanding of color (Newton, 1672, 1952). By passing sunlight through a glass prism, Newton showed that white light is composed of rays of different wavelengths.

Using a second prism, he showed that the dispersed colors could not be further decomposed, demonstrating that color originates in the spectral composition of light rather than being generated by the prism. These findings laid the foundation for modern optics (Mollon, 2003).

Thomas Young hypothesized the trichromacy theory which states the existence of three types of photoreceptors in the retina which have their peak in different part of the light spectrum (Hermann von Helmholtz, 1852; Young, 1997). The appearance of light can therefore be described as a point in a three-dimensional space.

The great merit of Young was to establish that trichromacy was not a physical property of light but a physiological property of the human visual system.

James Clerk Maxwell (Maxwell, 1857) fundamental contribution came from a device that could match daylight with combinations of three monochromatic lights. His experiments demonstrated that most colors can be matched by superimposing light from three different color sources or "primaries". His contributions ultimately led to the development of modern colorimetry.

Around 50 years after Young works, Hermann von Helmholtz used color matching paradigms to eventually prove the validity of the trichromatic theory. He developed the first mathematical model of color space combining experimental psychophysics and geometry (Von Helmholtz, 1867; Peruzzi & Roberti, 2023).

At this point, the theory of trichromacy presented some limitations concerning, for example, how color appearance is influenced by surround: the same color red, for example, would look different against a green or a grey background. Color, therefore, cannot be reduced to the activation of the red, green and blue color channels.

Interestingly, a prominent opponent of the trichromacy theory was Ewald Hering, who proposed an alternative framework based on the existence of four "unique" hues: red, green, yellow, and blue (Hering, 1878). These hues are considered *unique* because they are perceived as pure colors and not as mixtures of other hues. Hering further proposed that these four colors are organized into two antagonistic pairs, red versus green, and yellow versus blue, such that the perception of one color in each pair inhibits the perception of the other.

Although Hering's original claims about the perceptual primacy of these hues are not entirely correct, his opponent-process theory accurately describes the post-receptoral stages of color vision. It captures how cone signals are recombined into opponent channels within the visual system. Opponent-process theory is not, therefore, in conflict with trichromatic theory. They are complementary and describe different level of color processing. Vor Kries (von Kries, 1905) was the first to propose a unification of the two theories, followed by the contribution of Müller (Müller, 1924) and finally formalized by Hurvich and Jameson (Hurvich & Jameson, 1957).

While contemporary neuroscience has achieved incredible advances and has allowed us to precisely characterize the multiple stages of visual processing and its neural substrata, it is striking to think about the foundational work laid by scientists that came before technological progress. Their ingenious experimental designs and theoretical insights shaped modern color science.

An overview of the visual system: from retina to cortex

For humans, vision is the most important of the five senses. Its dominance seeps into our language *("See? That's what I was trying to explain."; "Let's see what happens."*), and it is reflected in the number of resources our brains utilize to process it. Around 60% of the neocortex is involved in visual processing.

The first step of vision is the absorption of light in the retina. Then, the optic nerve sends the visual information though the optic chiasm until it reaches the lateral geniculate nucleus (LGN) in the thalamus. This thalamic nucleus is divided in six layers, two inferior ones comprised of

magno-(*large*) cellular neurons, and four comprised of parvo-(*small*) cellular neurons. Even smaller cells make up the koniocellular layers, that lie between the other two types. From the LGN, visual information reaches the primary visual cortex (V1) through the optical radiation. The retinal and thalamic parts of the visual stream are generally well characterized. What is still highly debated is how the cortical visual areas encode the complex visual features they are presented with. The following section will provide a more detailed discussion of the visual processing pathways.

Color in the retina

Color vision in humans begins at the retina. The retina is a sensory membrane that lines the back of the eyeballs, and it contains three types of light sensitive cells commonly named cones. These cells, also known as photoreceptors, are sensitive to different ranges of the visible spectrum. They are referred to as long- (L-), middle- (M-), and short- (S-) wavelength–sensitive cones. Each cone type expresses a distinct opsin photopigment, with peak sensitivities at approximately 420 nm, 530 nm, and 560 nm (P. K. Brown & Wald, 1964; Stockman & Sharpe, 2000). The characterization of the cone spectral absorption function, now so easy to access, is the result of a combined effort spanning over a century and one of the hallmarks of color vision (König & Dieterich, 1892; Smith & Pokorny, 1975; Stockman & Sharpe, 2000).

The three photoreceptors are sometimes called red, green and blue cones, although this is technically incorrect. While the "blue-" and "green-sensitive" cones have their peak sensitivities in the violet-blue and green parts of the spectrum respectively, the so-called "red-sensitive" cones have their peak sensitivity in greenish yellow, not red. More importantly, individual cone cell types don’t detect color, or a specific wavelength. The L- and M- cones are sensitive to all wavelengths of visible light, and while each respond to different parts of the spectrum to different degrees, their response alone is ambiguous, because it simply encodes the absorbed photon count. This means that a higher response from a cone could be caused by a shift of the light’s wavelength toward the cell’s peak sensitivity, an increase of intensity, or a combination of the two. Color vision therefore is based on the comparison of the signals from the cones.

The representation of a color sensation is three-dimensional, or “trichromatic”. Amongst mammals, only humans and some Old-World primates possess three classes of cones, while the rest have two, making their color vision “dichromatic”.

A remarkable characteristic of the cone sensitivity is the overlap between L- and M- cone absorption spectra. Their peaks are only 30nm apart, resulting in a high correlation between their signals.

This is possibly the consequence of both evolutionary constraints and functional requirements of the visual system.

From an evolutionary point of view, L- and M- cones became distinct "only" 30 to 40 million years ago from a common ancestor and remain, therefore, very similar.

Functionally, this overlap represents a compromise. We don't only extract chromatic information from a scene, but from luminance, too. The visual system relies on combining the signals from L- and M- cone compute to luminance information. Because the strength of chromatic signals increases with greater separation between cone spectral sensitivity, the closeness of L- and M-cones minimizes chromatic contamination of luminance signals (Gegenfurtner & Kiper, 2003; Osorio et al., 1998).

This could also explain why cones are distributed unevenly across the retina: there is a high concentration of L and M cones in a small, central pit area of the retina called fovea, while S cones are almost completely absent there (Curcio et al., 1991). The fovea provides the sharpest visual acuity.

S cones account for only 5-10% of all cones and reach their maximum concentration at around ~1° eccentricity (Curcio et al., 1991; de Monasterio et al., 1985; Marc & Sperling, 1977). L-cones generally outnumber M-cones in a ratio that varies among individuals from approximately 1:1 to nearly 4:1, although this appears to have only a minor impact on color perception (Brainard et al., 2000; Roorda & Williams, 1999). Furthermore, L- and M- cones are distributed randomly across the mosaic, so it is common to observe clumps of cones of one type (Roorda & Williams, 1999).

Signals from the cones are transmitted via bipolar cells to retinal ganglion cells (RGCs) in the optic nerve. There are three types of RGCs: parasol, midget and small bistratified cells, otherwise known as M, S and K cells. (Field et al., 2010). These signals are combined in three anatomically and functionally distinct pathways, representing the three cardinal directions of color vision. These axes encode luminance, red-green opponency, and yellow-blue opponency (De Valois et al., 1966; Derrington et al., 1984; Krauskopf et al., 1982).

Evidence for cone opponent responses in the LGN was first discovered by De Valois and colleagues (De Valois et al., 1966), who assumed that these response from the color sensitive cells in the LGN aligned with Hering's color opponent theory (Hering, 1964). They found

neurons excited by red light and inhibited by green light, and vice versa, as well as for yellow-blue light, and for presence or absence of mixtures of light.

This opponency originates from the input of the cones. We will take the red-green channel as an example: here, L and M cones output are computed by their difference such as L-M (excitatory input from L- cones, inhibitory from M- cones) and M-L (excitatory input from M-cones, inhibitory from L- cones). Similarly, in the yellow-blue channels the cones outputs are encoded as S-(L+M) and (L+M)-S. Finally, in the luminance channel the outputs of the cones are the sum of L+M.

These three cardinal mechanisms of color have been identified through psychophysical experiments as well (Krauskopf et al., 1982). They habituated subjects to a color along one of the cardinal directions and showed that detection performance was affected by colors along the same axes, but not the others. Interestingly, the colors of the cardinal directions don't exactly overlap with Hering's unique hues (the blue-yellow axis is more purpleish-greenish) like shown by De Valois. (De Valois et al., 1966).

Color in the LGN

RGCs transmit to the lateral geniculate nucleus (LGN) in the thalamus and to the superior colliculus.

The three pathways project to a specific set of layers in the LGN, from which the pathways take their names: magnocellular, parvocellular and koniocellular (Dacey, 2000; Dacey & Packer, 2003; De Monasterio & Gouras, 1975; De Valois et al., 1966; Perry et al., 1984; Wiesel & Hubel, 1966).The magnocellular layers of the LGN receive input from M cells. Their signal is the sum of L- and M- cone output. The receptive fields of M cells are circular and divided into spatially antagonistic centers and surrounds. For example, ON-center cells will receive excitatory input in its center from both L- and M-cones while the surround receive inhibitory signals. OFF-center M cells receive inhibitory signals in the center, and excitatory signals in the surround. Magnocellular neurons in the LGN have high luminance contrast sensitivity and high temporal resolution. They also have low spatial resolution due to their relatively large receptive fields and are largely insensitive to chromatic differences (Croner & Kaplan, 1995; Crook et al., 2008; Kaplan & Shapley, 1986). Compared to the parvocellular pathway, they have lower retinal distribution density (Perry et al., 1984).

These characteristics make them the most sensitive to luminance and motion information.

The parvocellular pathway corresponds to the red-green cardinal mechanism. The red–green opponency is generated by the weighted differences between L- and M-cone signals. This information is conveyed by midget ganglion cells (P cells), which in the fovea often receive input from a single cone via a single midget bipolar cell (B. B. Lee et al., 2010). Most of their receptive fields are color-opponent center-surround, with either L-ON/M-OFF or M-ON/L-OFF polarity. The parvocellular path has a much higher density of neurons compared to the other two. Each L or M cone in the fovea thus contributes to both an ON-center and an OFF-center midget ganglion cell, yielding four distinct receptive field types: L-ON, L-OFF, M-ON, and M-OFF (Derrington et al., 1984; Dreher et al., 1976; B. B. Lee et al., 1997). Neurons in the parvocellular layer have small receptive fields, lower contrast sensitivity and high spatial resolution.

The third pathway (Casagrande, 1994; Hendry & Reid, 2000), mediated by K cells, carries signals computed from the difference of the S-cones input and the weighted sum of L- and M-cones signals (Dacey, 1993; Dacey & Lee, 1994; Rodieck, 1991).

These three LGN pathways provide parallel input to the primary visual cortex via the optic radiation.

Interestingly, this connection is not a simple feedforward process, as there is a great source of input coming from corticogeniculate neurons of the primary visual cortex back to the LGN (Erişir et al., 1997).

Color in the cortex

In the visual cortex, the projection from the LGN magno, parvo and koniocellular pathways terminates in different layers of the primary visual cortex (Merigan & Maunsell, 1993; Callaway, 1998). Magnocellular inputs primarily target layer 4Cα (Chatterjee & Callaway, 2003), parvocellular inputs terminate mainly in layer 4Cβ (Fitzpatrick, 1996; Lennie & D'Zmura, 1988), and koniocellular inputs project to layers 1 and 2/3, including cytochrome oxidase (CO) blobs (Chatterjee & Callaway, 2003; Sincich & Horton, 2005a).

As the visual signal reaches the cortical areas, it becomes evident that the pathways from the LGN are not as clearly segregated anymore, with higher cortical areas displaying intricate interconnections (Sincich & Horton, 2005b).

Nonetheless, several models propose that functionally distinct pathways remain relatively segregated through the extra-striate hierarchy (DeYoe & Van Essen, 1985; Hubel & Livingstone, 1987; M. S. Livingstone & Hubel, 1987; Roe & Ts'o, 1999).

According to this segregation hypothesis, independent processing of visual attributes is preserved from the retina through the LGN and into higher cortical mechanisms, implying the existence of specialized cortical systems devoted to specific visual features such as color, form, motion (M. Livingstone & Hubel, 1988).

Livingstone and Hubel published well-known studies investigating the neurons of V1 and V2 (M. Livingstone & Hubel, 1984, 1988; M. S. Livingstone & Hubel, 1987) and based on their results, they drew conclusions in support of this modular view. A key part of their argument are the so-called "double opponent" cells (Daw, 1968). These neurons compare signals from different cone types and compare color signals across different locations in space, such that they respond when their receptive fields centers are stimulated with one color and their surround with the opponent color (M. S. Livingstone & Hubel, 1987; Conway, 2001; Daw, 1968). This makes them sensitive to local color contrast. These types of cells were found mostly in a hypothesised and segregated color channel within CO rich compartment of V1 of and V2. In addition, Ts'o and Gilbert identified clusters of neurons in the CO-blobs of which displayed color opponent mechanisms along red-green and blue-yellow directions. (Ts'o & Gilbert, 1988).

Notably, though, neurons of primates V1 respond not only to the cardinal directions but to mixed colors too (Conway, 2001; Lennie et al., 1990; Solomon & Lennie, 2007), and so do the cells of extrastriate visual regions (Gegenfurtner et al., 1996, 1997).

Furthermore, the segregation of color processing identified within V1 and V2 remains controversial, as other studies did not find such evidence (Gegenfurtner et al., 1996; Leventhal et al., 1995; Levitt et al., 1994). They found that V2 and V3 share similar proportions of color selective cells (respectively, 50% and 54%) and that in V3 there is a significant interactions between color and motion processing, rather than being segregated (Gegenfurtner et al., 1996, 1997).

Is there a color center in the brain?

A framework that attributes specific features to distinct brain areas has been the predominant one for decades.

Semir Zeki was a strong supporter of the modular view (Shipp & Zeki, 1985, 2002; S. M. Zeki, 1978). He proposed that motion processing proceeds from V1 to area to extrastriate visual area V5, also called the middle-temporal area (MT) (Shipp & Zeki, 1985; S. Zeki, 1980). According to his results, neurons in this area were, for the majority, directionally selective.

Color information, on the other hand, would be processed by the numerous color-selective neurons in extrastriate visual area V4 (Essen & Zeki, 1978; S. Zeki, 1983a).

The claim that macaque V4 possess the highest percentage of color sensitive neurons, making it the "color center", was later disproved, with more studies showing that V4 is similar to the other cortical areas in term of color sensitivity (S. Schein et al., 1982; S. J. Schein & Desimone, 1990). In general, V4 seems involved in the process of shape and luminance as well, if not more, than color (Desimone et al., 1985; Desimone & Schein, 1987). Furthermore, lesion studies showed that damaging macaque V4 cause only mild deficit to color perception (Cowey & Heywood, 1995).

The idea of a corresponding color center in the human brain has been studied extensively by Zeki and colleagues (Bartels & Zeki, 2000; Lueck et al., 1989; S. Zeki, 1990), motivated particularly by the phenomenon of cerebral achromatopsia, a deficit that affects the ability to recognize color, but leaves intact the perception of form and motion. In reality, these deficits are hardly purely about color, but seems to involve other clusters of deficits as well, including the ability to recognize faces (Bouvier & Engel, 2006).

Characterizing the visual system as made of strictly parallel and independent streams for different features appear reductive, given the incredible evidence in favour of its complexity. Therefore, it seems unlikely that the brain would have an area dedicated to the sole task of processing color. Rather, visual processing is the result of simultaneous activity across different cortical locations.

The role of V1 in color perception

The role of the primary visual cortex in color perception was underestimated, as earlier studies found that only a small percentage of its neurons was color selective.

Zeki initially assumed that V1 didn't really respond to color stimuli (S. Zeki, 1983a, 1983b).

As described above, Livingstone and Hubel had identified double-opponent cells as responsible for the initial stage of color processing in the cortex but didn't offer evidence that these cells were more sensitive that cells in other V1 layers.

Lennie (Lennie et al., 1990) hypothesised that the only color cells in V1 were the ones that respond more strongly to equiluminant than to black and white stimuli.

More studies on V1 have revealed that neurons of macaque V1 are typically selective for multiple visual features. Color-selective neurons are just as orientation- and direction-selective as non–color-selective neurons, arguing against strictly specialized "color" cells (Leventhal et al., 1995). Similarly, Friedman and colleagues (Friedman et al., 2003) showed that color, orientation, and edge information are multiplexed in V1 and V2: most color-selective neurons in upper V1 layers were edge- and orientation-selective, only a smaller subset responded to uniform color surfaces, and correlations between color sensitivity and orientation selectivity were weak or slightly positive, contradicting the modular hypothesis and closely matching earlier findings from Leventhal (Leventhal et al., 1995).

Johnson and colleagues (Johnson et al., 2001) classified neurons of V1 in three categories: luminance-preferring, color-luminance, and color-preferring cells. Later work (Johnson et al., 2004) showed that most color-luminance cells were double-opponent, supporting a role in spatially detailed color processing, while color-preferring were likely single opponent. Human VEP studies further support this view by showing that cortical color responses are spatially tuned and dominated by mechanisms similar to color-luminance cells rather than low-pass color-preferring cells (Girard & Morrone, 1995; Rabin et al., 1994).

Taken together, these results suggest that V1 plays an important role in the processing of color information thanks to the contribution of single and double opponent cells (Johnson et al., 2008; Shapley & Hawken, 2011).

In their review, Gegenfurtner and Kiper discuss that discrepancies in identifying the number of neurons involved in color processing might be cause by the classifying method (Gegenfurtner & Kiper, 2003). For example, many early studies relied on qualitative or binary classifications (e.g., color vs. luminance, oriented vs. unoriented), even though individual neurons often

encode multiple stimulus attributes (Leventhal et al., 1995). If we change how we define a "color neuron" definition, we can draw different conclusions: we find more color cells because the definition is not binary, but rather cells fall on a spectrum.

A more integrated view of the visual system challenges the notion of a "color center" of the brain. Although area V4 plays an important role in color processing, its neurons do not respond more selectively to color than neurons in other visual areas. Moreover, V4 was considerate the key of how our visual system achieve color constancy, the ability of recognize the correct appearance of colors under different illumination. The discovery of double-opponent cells in V1 proved that computations to achieve the perception of color constancy happens in early visual stages.

As mentioned above, a key concept of the modular view is the separation of color and motion processing, which are thought to be mediated by the extrastriate areas V4 and V5, respectively (Shipp & Zeki, 1985; S. Zeki, 1980; S. M. Zeki, 1978).

However, what Gegenfurtner and Hawken found is that these mechanisms are not strictly separate. Instead, they suggested the existence of two motion mechanisms that process both luminance and chromatic information but differ in their temporal characteristics (Gegenfurtner & Hawken, 1995, 1996a).

The emerging view is therefore that color perception arises from the distributed and simultaneous activity of neurons across multiple cortical areas. While some degree of anatomical segregation exists, there is little evidence for strict functional segregation (Gegenfurtner & Kiper, 2003; Lennie et al., 1990; Shapley & Hawken, 2011)

Overall, the modular view has the advantage of providing an intuitive framework that links psychological concepts such as color or motion perception with its corresponding neural substrate. It shouldn't, though, limit how we continue to investigate. As Shapley and Hawken highlighted in their review (Shapley & Hawken, 2011), the idea that color is processed separately from other features is still incredibly present and engrained despite the numerous evidence suggesting a more nuanced view than simple parallel streams.

Perception in action

So far, we have discussed how color is processed at the different stages of our visual system: we are still far from a perfect understanding of how the brain sees color, but it is reasonable to assume it's not processed in isolation, but it is integrated with other visual features at early cortical stages.

The debate between modular and integrated views of cortical processing reflects a broader attempt to explain the mechanisms underlying perception and action.

Early experimental was concerned with the relationship between perception and action. Nineteenth-century theorists such as Wundt, James, and Ziehen viewed perception, motor behaviour, and conscious experience as deeply interconnected and theorized hierarchical accounts of sensorimotor control (Neumann & Scheddin, 1990).

Addressing this question is inherently complex and it requires theoretical and empirical work to come close to a definitive conclusion.

In 1992, Goodale and Milner proposed a theory that sees sensory information being processed by two distinct pathways, one for perception and one for action (Goodale & Milner, 1992).

They argue that, from an evolutionary point of view, conscious perception evolved as a later, representational system to model and interpret the world, while the original function of vision was to guide action directly, making perception and action functionally distinct rather than serial (Goodale et al., 2005).

An anatomic dissociation of the neural substrate for perception and action was first found in rodents (Schneider, 1969) and later in primates (Ungerleider & Mishkin, 1982).

Ungerleider and Mishkin identified two major sets of nerve projections in the monkey brain, both beginning in primary visual cortex. The ventral pathway projects into the temporal lobe and includes parts of V2, V4, and inferotemporal cortex. It's involved with processing what the objects are (their shape, size, and color). In other words, it identifies what the object is and plays a "vision for perception" role. The other pathway, the dorsal pathway, projects into the posterior parietal cortex and includes areas V3, MT, and the middle-superior-temporal area (MST). It deals with the analysis of where the target is located and their motion, forming a network in charge of "vision for action". They observed that by lesioning one of the pathways, the animal would lose one ability and not the other, and vice versa.

Despite its intuitive appeal and apparent simplicity, this dichotomy has been challenged by numerous findings revealing the complexity of visual processing. Firstly, vision is not a simple

feedforward process, but a complex, interconnected network (Felleman & Van Essen, 1991). Areas belonging to both streams proved to process information about the "what" and "where" of objects, such as shape (Konen & Kastner, 2008) and color (Claeys et al., 2004) being processed in the dorsal stream. Similarly, there is neurophysiological evidence of the ventral stream processing motion information (Gur & Snodderly, 2007).

The division of perception and action finds more arguments in neurological patients displaying a double dissociation between the two caused by lesions. Visual agnosia patients, with lesions in the ventral pathway (Grill-Spector, 2003) are described as unable to recognize object, but can point or grasp them. On the other hand, lesions at the dorsal stream can identify and name objects correctly but fail when it comes to visually guided motor actions (Culham & Valyear, 2006).

When it comes to draw conclusions from clinical studies, it's important to recognize that every patient is unique in their clinical history and their symptoms. Deficits rarely map cleanly onto a single or neural function, making it difficult to attribute specific impairments unambiguously to damage in a particular network. Indeed, these two neurological conditions present deficits that can be explained by different interpretations (Pisella et al., 2009; Rossetti et al., 2003). Many optic ataxia patients can perform accurate visuomotor actions under specific conditions (e.g., central vision, delayed responses), while visual agnosia patients can show improved perceptual performance during action, indicating substantial interaction between perceptual and motor processes. clinical, behavioural, and neuroimaging findings suggest that performance deficits depend more on task demands, timing, and integrative requirements than on strict dorsal/ventral stream separation.

In healthy populations, the division between perception and action is supported by psychophysical experiments employing visual illusions: to put simply, visual illusions would influence perceptual judgments and motor responses in different ways (Aglioti et al., 1995; Bridgeman et al., 1981; Coello et al., 2007; Gentilucci et al., 1996), suggesting that while perception (aka the ventral stream) is affected, tasks dominated by the dorsal stream are "immune" because it can't access the perceptual knowledge processed in the ventral stream. The act of grasping was often used as the representative motor task, as the finger aperture represented the perceptual representation of the stimulus size transformed into a motor command.

Similarly, masking paradigms are proposed as further evidence for a perception and action division, based on the principle that while vision for perception is conscious, vision for action may not be (Milner & Goodale, 2008). These studies showed that primes or distractors that fail

to reach conscious awareness can still modulate reaction times and the reaching movements (Bernstein et al., 1973; Taylor & McCloskey, 1990; Van der Stigchel et al., 2009).

This conclusion has been weakened by subsequent work (Bruno et al., 2010; Bruno & Franz, 2009; Franz, 2001); (Kopiske et al., 2016). A major criticism is methodological: perceptual and motor tasks were often not properly matched, differing in stimulus presentation (simultaneous vs. sequential), response demands, and timing, all of which can modulate illusion strength (Franz et al., 2000). Indeed, when tasks are carefully controlled to be comparable, there are no difference between perceptual an motor tasks (Franz & Gegenfurtner, 2008). Furthermore, what count as perceptual vs motor task is often ambiguous, with some measures such as finger aperture serving as either depending on context.

Interestingly, Kleinholdermann and colleagues (Kleinholdermann et al., 2009) tested whether an object's chromaticity alone was sufficient to perform a grasp movement. If the theorized dorsal stream had little or no access to color information, grasping an equiluminant target should be partially impaired compared to a luminance defined one. Their results didn't find a significant difference, further evidence for a more integrated view of the visuomotor system.

What seems more plausible is that these behavioural dissociations result from different processing demands of what is designed as perceptual and motor tasks (i.e., immediate vs delayed) (Rossetti et al., 2003).

The framework provided by an anatomical and functional separation of perception and action has dominated the scientific landscape for the past decades. This has led to great new discoveries, both through findings that support this distinction and through evidence that challenges its limits and reveals interactions between the two systems.

This work presented in this thesis aligns with an integrated view of perception and action. In our view, perception is intrinsically linked to action. Our representation of the visual world includes not only information about objects and scenes, but also about goals, plans, attentional priorities, and expected rewards. Color vision therefore plays a role not only in perception but also in guiding behaviour.

How motor behaviour is planned and executed is relatively well characterized (Rizzolatti et al., 1998), but we need a better understanding of how sensory information is transformed into motor commands.

The oculomotor system offers a useful model for studying the dynamics of perception and action. It has a well-defined neural circuitry and produces precise, quantifiable behavioural outputs, making it ideal for investigating how visual information guide action. In the next

section, I will discuss the neural basis for eye movements and how they relate to color processing.

Eye movements

The simplest visually guided action we can do is moving the eyes. Scientific study of eye movements began in the late 19th century, when technological advances allowed reliable measurement of eye position (Buswell, 1935; Huey, 1900; Orschansky, 1899; Yarbus, 2013).
Eye movements are driven by a complex system of cortical and subcortical network: for saccades, the pattern of neural activity is shaped by the brainstem, where "omnipause" and "burst cells" work together to control when a saccade starts, how fast it is, and when it stops (Leigh & Zee, 2015; Sparks, 2002; Sparks & Barton, 1993; Wurtz & Goldberg, 1989). Both types of cells receive signal from the superior colliculus (SC), a high center of the mid brain involved in the control of eye-movement. The SC receives visual input from several cortical region as well as direct input from the retina and these connections make it a fundamental visuomotor center for eye movements. The two principal cortical input to the SC come from the frontal eye field (FEF) region and the posterior parietal cortex.
At the cortical level, saccades are influenced by a distributed network that contributes sensory, attentional, and motor-related signals (Findlay, 2009). Two of the principal cortical inputs to the SC originate from the frontal eye fields (FEF) and the posterior parietal cortex. The FEF plays a central role in voluntary saccade initiation, target selection, and the control of saccade metrics, and can evoke saccades when stimulated directly (Hanes et al., 1998; Hanes & Wurtz, 2001). In contrast, regions of posterior parietal cortex, including the lateral intraparietal area (LIP), are thought to encode spatial representations of potential saccade targets and to integrate visual, attentional, and task-related information (Barash et al., 1991). Additional contributions come from supplementary and cingulate eye fields, which are implicated in internally guided saccades and decision-related aspects of oculomotor control. Through their convergent projections to the SC and basal ganglia, these cortical areas influence which targets are selected for action and when a saccade is executed, linking perceptual processing to motor execution.
Smooth pursuit eye movements rely on partially overlapping cortical circuits (Krauzlis, 2004; Orban de Xivry & Lefèvre, 2007) that emphasize continuous visual motion processing. Both types of eye movements work synergically to track the visual target. Visual motion signals originate in early visual cortex and are elaborated in extrastriate areas such as MT and MST, which encode the direction and speed of moving stimuli(Newsome & Pare, 1988). These

signals are then relayed to pursuit-related regions of the frontal eye fields and to posterior parietal areas, where visual motion information is transformed into motor commands that match eye velocity to target motion. At the subcortical level, pursuit signals are conveyed through pontine nuclei and the cerebellum before reaching oculomotor nuclei in the brainstem. Here, I presented a quick overview of the neural circuits of eye movements. In the following section, I will go into detail into the interactions of color and luminance processing and eye-movements.

Color processing and eye movements

Color and luminance sensitivity are modulated by eye movements. Interestingly, it was believed that color signals were not present in neural circuits involved saccadic eye movements (Marrocco & Li, 1977; Ottes et al., 1987; Schiller et al., 1979; Schiller & Malpeli, 1977) and thought to be mainly driven by luminance information (Schiller et al., 1979). The visual cortex, projects directly and indirectly through an intricate network of connections to saccadic substrates, in particular the superior colliculus (SC), including inputs from areas involved in the processing of color (Fries, 1984; Lock et al., 2003; Lui et al., 1995). Furthermore, behavioural findings challenge the notion that the saccadic system is insensitive to color. Human observers can detect and orient their saccadic eye movements toward chromatic stimuli that are isoluminant with the background (White et al., 2006). Clearly, the SC receives input from the magno- and parvocellular pathways. Visual onset latencies for chromatic stimuli have been found to be 30-35 milliseconds longer than for luminance (Barbur et al., 1998; White et al., 2009), which is compatible with the sustained and slightly delayed visual onset latencies in neurons from the parvocellular layers of the LGN (Maunsell et al., 1999) as well as with the larger latency differences reported between magnocellular and parvocellular input layers in V1 (Nowak et al., 1995).

Beyond these differences in response latency, eye movements themselves also modulate visual sensitivity.

During saccades, visual sensitivity is transiently suppressed (Burr & Ross, 1982; Ross et al., 2001). This happens because during a saccade the image of the world projected on the retina moves incredibly fast, so lower sensitivity helps to maintain perceptual stability. Evidence suggests that this suppression is strong particularly for rapid, low-frequency luminance modulation, consistent with suppression of magnocellular processing (Schwartz & Godwin,

1996), while sensitivity for chromatic and high-spatial frequency luminance stimuli is mostly unaffected.

While there is numerous evidence documenting this effect (Burr et al., 1982, 1994; Ross et al., 1996; Uchikawa & Sato, 1995), it is possible that this mechanism is more complex than previously thought: Braun et al. (D. I. Braun et al., 2017) found saccadic suppression for luminance, and a weaker, but significant, suppression for chromatic targets too. Furthermore, Zhang et al. (Zhang et al., 2024) found that the neural correlates of saccadic suppression in the primary visual cortex are similar for luminance and chromatic stimuli, suggesting a generalized suppression of the early visual system sensitivity that affects the parvo- and magno- cellular pathway alike.

During smooth pursuit, a different trend emerges: the sensitivity for low-spatial frequency luminance is mostly unaffected, while for chromatic and high-frequency luminance stimuli is increased. Schutz et al (Schütz et al., 2008) suggest that this enhancement might origin in a boost in the parvocellular pathway, as a way to reduce motion blur for stationary objects and increase sensitivity to speed changes of the moving target(D. I. Braun et al., 2017; Schütz et al., 2008, 2009). This effect is found in behavioural data(D. I. Braun et al., 2017; Schütz et al., 2008) and is corroborated by physiological results as well, with enhancement is SSVPs amplitude to chromatic flicker during pursuit (Chen et al., 2017). During the execution of smooth pursuit, we also observe enhancement in the temporal resolution of chromatic stimuli processing due to cortical mechanisms (Terao et al., 2010).

Together, these findings suggest that visual sensitivity is not uniformly suppressed during eye movements, but rather reweighted depending on the type of movement and the stimulus properties.

These differential modulations raise important questions about how color signals are integrated within oculomotor circuits.

Chapters Overview

The present work will focus on understanding how color is perceived and how color information interacts with other aspects of visual and sensorimotor processing. It spans both fundamental questions about the temporal dynamics of color vision and higher-level questions about how perception is shaped in active contexts.

In one study, we used eye-movements as a tool to investigate the temporal characteristic of cones and how they influence the way we perceive the brightness of color. In the second work, we investigate color discrimination using a task that keeps observers engaged and physically active to explore the consequences of perception under action.

In the first study we investigated how different characteristics of color influence eye movements. To do this, we asked participants to choose the brighter color between two stimuli by directing their gaze towards the target.

In perceptual science, how "bright" a color appears is described in terms of its luminance.

The luminous efficiency function V(λ) describes how sensitive the human visual system is to the wavelengths of the visible spectrum. The luminance of a light is calculated by summing its radiance, across wavelengths, with each wavelength weighted by V(λ).

It was established by the Commission Internationale de l'Eclairage (CIE) in 1924 and it is one of the great success stories of visual science (CIE, 1926)

One of its limitations though is that luminance doesn't align with color brightness perception. Two colors that appear equally bright to our eyes, likely won't have the same luminance. This is particularly true for colors like yellow and blue: if we observe an equiluminant yellow and a blue light, the blue one appears much brighter than the yellow one.

This happens because short-wavelength-sensitive cones seems contribute little to luminance compared to long- and middle- wavelength sensitive cones (Cavanagh et al., 1987; Eisner & MacLeod, 1980; J. Lee & Stromeyer 3rd, 1989; Stockman et al., 1987; Verdon & Adams, 1987), despite, of course, contributing to color brightness perception.

Furthermore, previous literature suggested that signals from the S-cones are processed more slowly compared to L and M cones (McKeefry et al., 2003; Smithson & Mollon, 2004). Studies on reaction times show longer latencies for stimuli defined by short wavelength light (Mollon & Krauskopf, 1973), and temporal sensitivity measurements show delays for S-cone isolating modulations (Shinomori & Werner, 2008). Furthermore, the response to S-cone stimuli decline

more rapidly in early human visual cortex with increasing temporal frequency compared to L- and M- cone stimuli (Spitschan et al., 2016).

Our results aligned with this distinction. We focused on the latencies of saccades and smooth pursuit eye movements. We asked participants to direct their gaze towards one of two colored circles, one blue and one yellow, based on which one they perceived as brighter.

When participants had to pick between an equiluminant yellow and blue pair, the fastest eye movements were driven almost entirely by luminance and showed no preference between the two colors. As latencies became longer and the visual system had more time to process the input from the S cones, the blue target was selected more often than the yellow one. The distribution of the latencies for both saccades and smooth pursuit clearly show a relationship between the speed of the eye movement and brightness preference: longer latencies correspond to higher selection of the blue equiluminant target, suggesting that S- cones contribute more to this perceptual decision.

Overall, these results highlighted the distinct temporal characteristics of the mechanisms that process color, and they showed how these differences became evident in the way the eyes selected and responded to visual targets.

The second study adapted a classic color discrimination paradigm, an alternative-forced choice task, to a gamified VR setting. As a result, we showed two important achievements. By introducing the gamifying aspect to the task, we created a valid methodology for making large-scale data collection more feasible. Secondly, we showed that perceptual tasks can be performed under active conditions, yielding results that are equivalent to classical psychophysical experiments.

Measuring color discrimination thresholds across the full three-dimensional color space is extremely demanding, as the space is vast, sensitivity varies with direction and location, and the number of required measurements grows exponentially with dimensionality. Classic studies by MacAdam and Brown (W. R. J. Brown & MacAdam, 1949; MacAdam, 1942), for example, required thousands of measurements collected over 18 months from a single observer.

To address this challenge, we developed a new paradigm that implemented fast and engaging data collection. The color discrimination task was performed as a VR computer game, where participants made rapid perceptual judgements while engaging with the virtual environment. Our results aligned with previous literature: color discrimination is not uniform across color space. For instance, observers detected smaller differences between orange-ish hue steps than orange-ish chroma, while this difference is less marked when judging purple-ish stimuli.

Most importantly, we showed that our VR-based method offered a highly efficient way to collect the large volume of data needed for mapping thresholds in three-dimensional color space. The gamified design favoured fast-paced trials and supported long testing sessions, since participants found the task engaging rather than tiring. Furthermore, this approach did not compromise data quality. We compared the thresholds obtained with the gamified task with results from a control study with condition resembling more a traditional psychophysics setting, and we didn't find significant differences.

Together, these research projects demonstrated both conceptual and methodological progress. First, we reveal how different components of color vision such as luminance and color processing influence visually guided behaviour over time. Second, we show that immersive VR and gamified tasks can provide high-quality perceptual data while enabling large-scale and multidimensional measurements.

Overall, both projects highlight the value of studying perception in the context of action, emphasizing how sensory processing and behaviour are connected.

II. Dynamics of S-cone contributions to the initiation of saccadic and smooth pursuit eye movements

Introduction

Luminance is a fundamental quantity that defines how efficiently lights with different spectral distributions stimulate the human visual system. For this purpose, the spectral distribution of lights is weighted by the luminous efficiency function V(λ). This curve was established by the Commission Internationale de l'Eclairage (C.I.E.) in 1924 (CIE, 1926) and has been a standard for business, science, and industry ever since. The V(λ) curve is defined mainly by flicker photometry, where visual stimuli are rapidly alternating at rates of about 30 Hz. However, one of the well-known drawbacks of V(λ) is its inability to capture the perceived heterochromatic brightness of most naturally occurring, non-flickering stimuli. Probably the biggest dissociation between luminance and perceived heterochromatic brightness occurs when comparing bluish and yellowish stimuli. For a yellowish looking stimulus to be equiluminant to a high intensity bluish one, its intensity needs to be lowered dramatically. The resulting light appears dark, drab brown, and much dimmer than the bluish one. The reason for this discrepancy is mainly that the pathways conveying signals from short-wavelength-sensitive cones (S-cones) do not contribute to luminance, because they are not very sensitive at the high temporal frequencies used in flicker photometry. However, they do seem to contribute to heterochromatic brightness (Ayama & Ikeda, 1998; Corney et al., 2009; Donofrio, 2011; Lennie et al., 1993; Mark D. Fairchild, 2013).

Here, we investigate whether oculomotor choice behavior is driven mainly by luminance, heterochromatic perceived brightness, or a combination of the two. Baker & Mollon (1993) specifically addressed this question for red-green stimuli and short-latency (express) saccades (M. Baker & Mollon, 1993). They found that it was mainly luminance that determined whether a particular stimulus was chosen over another one as the saccade target. We extend this study to different paradigms inducing a wide range of eye movement latencies, and used bluish and yellowish stimuli, where the difference between luminance and heterochromatic brightness is largest.

The detailed knowledge of the brain mechanisms that control voluntary eye movements

(Lisberger, 2015; Liston & Krauzlis, 2005; Munoz & Coe, 2011) allows us to link oculomotor neuronal activity to decision processes. We investigated the relationship between heterochromatic brightness perception and oculomotor behavior by measuring whether stimuli of different brightness or different luminance were preferably selected as targets for saccades and smooth pursuit eye movements. Both of these eye movements are essential to place the retinal image of a visual object of interest onto the fovea (Goettker et al., 2019; Lisberger, 2015; Schütz et al., 2009). Saccades achieve this by discrete, rapid movements of the eyes to the newly selected location of interest, while smooth pursuit keeps a moving target within the foveal region by continuous and relatively slow eye rotations at a similar speed and direction. Both types of eye movements are ideal for investigating the processing of visual signals and oculomotor decisions since their onset latencies are significantly shorter than manual responses such as button presses (Lisberger, 2015; Missal et al., 1996). Their latencies and metrics indicate which visual information is selected and relevant for the target selection, and how it is integrated and evaluated for the decision to execute an eye movement or not.

Eye movements are controlled by a hierarchy of circuits, originating at the retina and converging to the superior colliculus (SC). The SC is one of the key structures for oculomotor control that has been associated with the transformation of visual signals into motor commands for saccadic eye movements (Sparks, 1986; Sparks & Hartwich-Young, 1989). Activation in the maps of the intermediate and deeper layers of the SC determines the target location of the upcoming saccade. In addition to the direct route from the retina to the SC, there are circuits including primary visual cortex (V1), lateral intraparietal cortex (LIP), infero-temporal cortex (IT), frontal eye fields (FEF), and basal ganglia (Hafed et al., 2023; Krauzlis, 2005). These extended circuits lead to longer latencies (Schmolesky et al., 1998), but they do take into account additional information about color, objects, motion, action planning, or rewards (for review, see (Schütz et al., 2011)).

If luminance alone determines oculomotor behavior, then eye movements directed to colored targets equi-luminant with the background should not be possible. This is clearly not the case, either for saccades nor for pursuit eye movements. The accuracy and precision of saccades to targets defined by color only are as good as for luminance defined targets, but their latency is a bit longer (White et al., 2006, 2009), particularly for S-cones (Bompas & Sumner, 2008, 2011). It has been shown that pursuit eye movements can be initiated to moving equi-luminant targets, but that pursuit onset is delayed by about 50 ms (D. I. Braun et al., 2008; Gegenfurtner & Hawken, 1996b).

With respect to the SC, early studies have reported that the visual activity of SC neurons

depends on luminance only (Schiller et al., 1979; Schiller & Malpeli, 1977). The superficial SC layers did not seem to receive inputs from S-cones (Marrocco & Li, 1977). Therefore, S-cone stimuli were assumed to be invisible to superficial SC neurons, compromising orienting behavior in tasks that require collicular activity (Sumner et al., 2002, 2004). White and coworkers (2009) confirmed that neurons in the superficial SC layers showed indeed little color-related activity (White et al., 2009). However, neurons in the intermediate SC layers were highly sensitive to equi-luminant color stimuli but responded with a short delay of 30-35 ms compared to luminance. About 14% of these neurons showed equal or greater responses in the S-cone direction than to the maximum contrast luminance stimulus. Hall and Colby (2014) directly recorded the activity of visual SC neurons in monkeys to S-cone-specific visual stimuli and found that most of these neurons were sensitive to the degree of S-cone contrast (Hall & Colby, 2014).

Given the significant role played by latency, we want to explore here the dynamics of color versus luminance information in oculomotor target selection. The idea is to induce eye movements, both saccades and pursuit, over a wide range of different latencies. For saccades, we used three different paradigms (gap, no gap, overlap), known to differentially activate different components of saccade planning (D. Braun et al., 1992; Saslow, 1967). For pursuit trials, we looked at the eye movement onsets, which were mostly pursuit movements, but sometimes saccades. This allows us to explore the dynamics of the contribution of luminance versus heterochromatic brightness for target selection. It is similar to the approach used by Schütz, Trommershäuser & Gegenfurtner (2012), who found that short latency saccades were driven by luminance alone, while longer latency saccades took into account information about reward as well (Schütz et al., 2012).

Our results show that for the equi-luminant yellowish and bluish stimuli, the target choice depends on latency. At the shortest latencies, equi-luminant bluish and yellowish stimuli were chosen equally often as targets for saccades and pursuit. As latency increased, the proportion of choosing bluish over yellowish stimuli also increased. Thus, short-latency eye movements are primarily driven by luminance, while longer-latency saccades and smooth pursuits are more determined by heterochromatic brightness, presumably due to a contribution of S-cones. The S-cone contribution was verified in a control experiment where we compared the yellowish stimulus to an equi-luminant purple stimulus that differed only in S-cone excitation.

Methods

For the saccade and smooth pursuit tasks, we used yellow and blue stimuli as competing targets to explore whether eye movements toward these chromatic stimuli are primarily driven by luminance or heterochromatic brightness. Specifically, we created pairs where the yellow and blue stimuli were equi-luminant, as well as pairs in which both stimuli were close to being perceptually equi-bright. This was to evaluate whether photometric luminance can serve as a useful metric for the initiation of eye movements. We were particularly interested in investigating if the mechanism responsible for eye movement target selection incorporates S-cone activity.

A. Participants

A total of 21 naïve observers (12 females, average age = 23.7, range 20–31 years) participated in the saccade task. Two observers had to be excluded because they did not follow the task instructions correctly. 17 observers (12 females, average age = 22.8, range 20–27 years) participated in the smooth pursuit task. 10 observers (9 females, average age = 26.7, from 23 to 32) took part in the S-cone isolated experiment, while one from the saccade experiment and two from the pursuit experiment were excluded due to their catch-trial accuracies being lower than 75%. All participants had normal or corrected-to-normal eyesight and normal color vision, as tested by the 24-plate edition of Ishihara plates (Ishihara, 2004). Before the experiment participants were informed about the procedures of the experiments and they signed written consent forms. The experiments were approved by the local ethics committee and agreed with the Declaration of Helsinki.

B. Apparatus

Stimuli were displayed on a 32-inch LCD monitor (Display++, Cambridge Research Systems Ltd., Rochester, UK) with a refresh rate of 120-Hz and a resolution of 1920 × 1080 pixels. The monitor had a visual angle of 45° (horizontally) × 25° (vertically) viewed at 85 cm and was calibrated by a CS-2000A spectroradiometer (Konica Minolta, Chiyoda, Tokyo, Japan). The R, G, and B channels had their CIE *xyY* coordinates at [0.645, 0.337, 25.885], [0.305, 0.603, 107.090], and [0.152, 0.065, 15.020], respectively. All the stimuli were present against a full-screen black background. All the experimental procedures were run by the Psychophysics Toolbox(Brainard, 1997; Kleiner et al., 2007) in MATLAB (Mathworks, Natick, Massachusetts, USA).

C. Experimental Paradigms, Stimuli and Procedures

Saccade experiment

In the saccade experiment, each trial began with the appearance of a fixation spot (diameter = 0.8°) at the center of the monitor for a variable duration between 100−1,000 ms(Krauzlis & Lisberger, 1994). Participants were instructed to maintain their gaze on the fixation spot and sound feedback was given if their gaze was not maintained within an area of 1.5 ° for 400 ms. If this occurred, the gaze drift would be automatically corrected by taking the median eye position, and the trial re-started. Three different paradigms were used for the temporal presentations of the fixation spot and the two targets: targets appeared immediately after fixation spot offset (no gap), they appeared after fixation spot offset with a 200 ms delay (gap), or 200 ms before fixation spot offset (overlap) (Fischer & Ramsperger, 1986; Saslow, 1967). The schematic diagram of the paradigms is shown in Figure 1.1A.

A blue and a yellow saccade target (diameter = 2°) were randomly positioned at an eccentricity of 4° at a 30° angle above and below the horizontal line, either on the left or right side of the screen. The chromaticities of the blue and yellow stimuli in CIE *xy* are [0.152, 0.065] and [0.403, 0.516]. There were three intensities each for blue and yellow, with RGB primary values set to 0.05, 0.15, and 0.485, resulting in 9 pairs with varying intensities. For the blue stimulus, only the blue primary was turned on at the given intensity. For the yellow stimulus, the red and green primaries were both turned on at the same given intensity. These parameters were chosen to ensure that the pair with yellow at 0.05 and blue at 0.485 had the same luminance (7.2 cd/m²), while the pair with yellow at 0.15 and blue at 0.485 had approximately the same perceived brightness (Guan et al., 2024). It is important to note that in the equi-luminant pair, the S-cone excitation of the blue stimulus (43.56%) was nearly 100 times as large as that of the yellow stimulus (0.44%). We specify cone excitations relative to those of the display white, i.e., when all primaries are fully turned on.

Participants were instructed to direct their gaze toward the brighter one of the two appearing target dots (that also appeared more visually salient) as fast as they could. When doing the task, eyes naturally orient towards one of the stimuli. Certainly, the short-latency saccades seem to be reflexive, and we would not expect that instructions would have much of an effect. This is evidenced by the example traces shown in Figure 1.1B, where initial saccades towards the yellow dots are always followed by subsequent saccades towards the blue dots. In our analysis, we define target selection by the direction of the first saccade made after target onset, disregarding subsequent eye movements occurring during the remainder of the trial.

We collected 288 trials for each paradigm (i.e., 32 repetitions for each pair), divided into 4 blocks, resulting in a total of 12 blocks. Data was collected over two different days and the order of the blocks was randomized by following a balanced Latin square design.

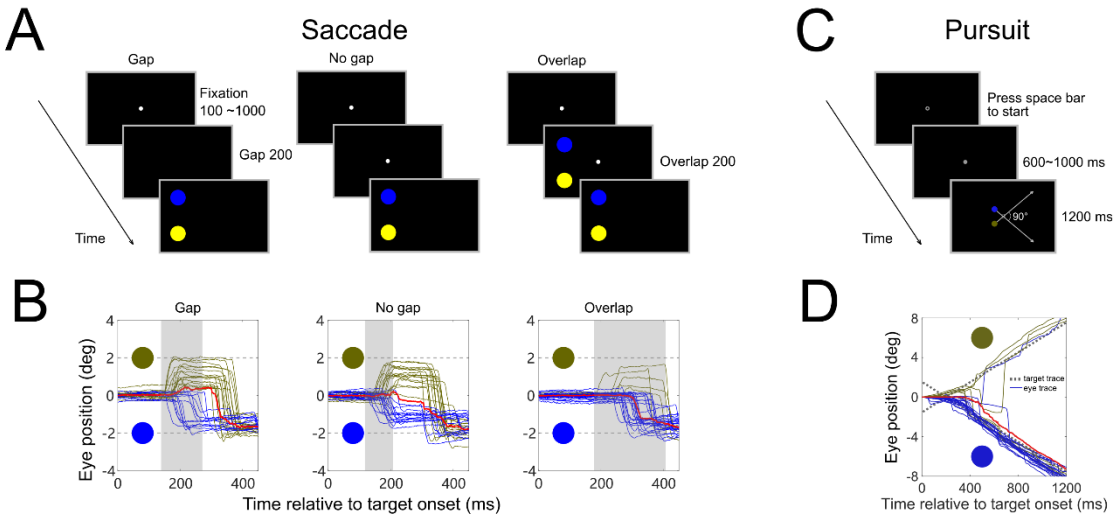


Figure 1.1. A. Experimental design of the temporal sequence of the presentation of the fixation and target stimuli in the saccade experiment. B. Saccade traces of a single representative participant for the equi-luminant stimulus pair. The red line represents the median gaze trace. The traces are colored based on the target selection, with yellow traces at the top and blue traces at the bottom. In each panel, the left edge of the gray shaded area indicates the onset of the saccade with the shortest latency, while the right edge indicates the one with the longest latency observed for that condition. C. Experimental design of the pursuit experiment. D. Pursuit traces of a single representative participant for the equi-luminant stimulus pair. Traces were colored with respect to the target selections of the participant during pursuit initiation, with yellow traces positioned at the top and blue traces at the bottom. The red line represents the median gaze trace.

Pursuit experiments

For our pursuit experiments, we adopted a step-ramp paradigm with two competing stimuli that has been used to study vector-averaging processes in pursuit initiation (Lisberger & Ferrera, 1997). Each trial began with a dark gray annulus presented at the center of the screen. Participants were asked to fixate on the dot at the center and to press the spacebar to start each trial. After the trial started, the annulus would fill in and remain at the center of the screen for 600−1,000 ms. When the annulus was completely filled, a yellow and a blue target (diameter = 0.8°) appeared at 1.5° in the opposite directions to their movement trajectories. Both immediately started moving into different diagonal directions, 45° upwards or downwards at a velocity of 10.6°/s for 1,200 ms (see Figure 1.1C). Participants were instructed to track the brighter of the two dots (that also appeared more visually salient) with their gaze as smoothly as possible.

Two experimental conditions were evaluated. In pursuit experiment 1 two yellowish stimuli (RGB primary intensities = 0.05 and 0.121) and two bluish stimuli (RGB primary intensities = 0.194 and 0.485) were used, resulting in four combinations. In Experiment 2 we aimed to find the point of oculomotor equality between the bluish and yellowish stimuli by fitting an oculometric function (Hawken & Gegenfurtner, 2001; Kowler & McKee, 1987) to the target choices. We kept the RGB primary intensity of the yellow stimulus at 0.05 and varied the intensity of the bluish stimulus between 0.05 and 0.485 in six equal steps in log space, resulting in the following linear values: 0.05, 0.079, 0.124, 0.195, 0.308, and 0.485. There were 40 repetitions for each condition, resulting in 160 and 240 trials in Experiment 1 and 2, respectively. The order of stimulus combinations was randomized. Participants had a break for at least 30 seconds after each block of 80 trials.

S-cone control experiment

In the above experiments, the bluish and yellowish equi-luminant stimuli differed mainly in their S-cone excitation, which was about 100 times higher for the bluish stimulus. However, since the relative excitation of L- and M-cones also differed, we cannot entirely exclude a potential contribution by a mechanism sensitive to the difference between L- and M-cones. Therefore, we designed a control experiment where we compared the yellowish stimulus to an equi-luminant purplish stimulus that differed only in S-cone excitation.

Experimental procedures were the same as above. Four pairs of stimuli were created. First, by keeping the L- and M-cone excitations of yellow constant and increasing only the S-cone excitation, we created a purplish stimulus with RGB values at [0.097, 0, 0.277], CIE *xy*Y coordinates of [0.202, 0.095, 7.008] and cone excitations of [4.56%, 4.33%, 24.95%]. This resulted in a 57-fold larger contribution from S-cones compared to the yellowish stimulus at an intensity of 0.05. Second, based on the CIE luminous efficiency function derived from the Stockman & Sharpe cone fundamentals (Sharpe et al., 2005; Stockman et al., 2008), we created a new bluish stimulus at an intensity of 0.395. Following an independently ongoing heterochromatic ranking experiment (Guan et al., 2024), we created two additional yellowish stimuli. In this heterochromatic ranking experiment (Guan et al., 2024), 144 patches comprising 12 hues and 12 intensities in RGB space were presented to observers, who were asked to rank them based on their perceived brightness. Using the RGB values and ranking data the optimal weights of RGB for heterochromatic brightness perception were determined by a max-weighted RGB model, with the weights being w_R: w_G: w_B = [0.40, 0.45, 0.15]. Based on these weights we created a yellowish stimulus at an intensity of 0.132 for the third pair. It

was equi-bright to blue at 0.395 according to these weights. For the fourth pair, another yellowish stimulus was generated at an intensity of 0.193. It was equi-bright to blue at 0.395, based on the raw ranking data of yellow and blue. Each of the four pairs was repeated 40 times in the pursuit experiment, and 22 times for each of the three saccade paradigms (gap, no gap, and overlap) in the saccade experiment. In addition, we combined a yellowish stimulus at 0.193 with a bluish one at 0.05 as a catch trial, in which the yellowish stimulus was much brighter than the bluish one. We presented these catch trials 20 times in the pursuit experiment and 33 times in the saccade experiment all together, (i.e., 11 repetitions for each saccade paradigm).

D. Eye movement recordings and analyses

All experiments were conducted in a dark room, with participants seated at a table and their heads resting on a chin and a forehead rest. The gaze from the right eye was recorded with a table-mounted eye tracker (EyeLink 1000 Plus, SR Research, Kanata, ON, Canada) running at a sampling frequency of 1,000 Hz. A nine-point calibration was done before each block and an additional drift correction at the beginning of each trial. Customized scripts in MATLAB were used to analyze offline all eye movement data.

For the data of the saccade experiment, saccades were detected by the EyeLink default algorithm with a velocity threshold of 30°/s and an acceleration threshold of 8,000°/s². Trials in which blinks occurred, or saccades landed within 0.5° around the horizontal midline were excluded from further analysis (excluded trials accounted for 0.6% of the total dataset). Target selection was determined based on the vertical eye position of the landing position of the first saccade, occurring within a time window of 100 to 500 milliseconds after target onset. For the equi-luminant target pair eye traces of a representative observer are shown in Figure 1.1B.

For the pursuit experiments in which the two targets moved vertically in two different directions, we analyzed the data of the vertical eye positions of our participants. First, we manually inspected the vertical eye traces of each trial. Trials were excluded if they contained blinks or missing data during eye movement initiation, resulting in the exclusion of 0.6% and 0.5% of trials in Experiments 1 and 2, respectively. Then, we followed the criteria described by Goettker et al. (Goettker, 2021) to identify smooth pursuit onset. Specifically, eye velocity was calculated by digitally differentiating the eye position over time and then it was smoothed using a second-order Butterworth filter with a 30-Hz cut-off frequency. When saccades were detected by the EyeLink, the eye movement velocity was linearly interpolated from −30 to 30 ms relative to saccade onset. Pursuit onset was defined as the first time point at which the eye velocity met the following two criteria: (1) the velocity exceeded three times the standard

deviation of the eye velocity during fixation (i.e., the mean velocity from −25 to 25 ms after target onset); and (2) the velocity remained above 30% of the target velocity for at least 10 consecutive samples (i.e., 10 ms). We used the sign of the eye velocity in a 40-ms interval after pursuit onset to determine the target selection direction (i.e., upward or downward). The example eye traces in response to the equi-luminant pair of a single observer are shown in Figure 1.1D. Although a step-ramp paradigm was used to achieve smooth pursuit initiation without any saccades (Rashbass, 1961), a small proportion of trials were still initiated by catch-up saccades. We followed the criteria described by Spering et al.(Spering et al., 2008) to classify pursuit and saccade trials. For valid pursuit initiations after target onset latencies had to be at least 60 ms and they had to start at least 40 ms before the first saccade. In Experiments 1 and 2, 58.9% and 65.1% of the trials were initiated by smooth pursuit movements, respectively.

E. Psychometric functions

In Experiment 2 of the pursuit task, we fitted psychometric functions to identify the weight of equi-bright yellowish and bluish targets during smooth pursuit initiation and to determine the PSE of oculometric brightness. We used a Weibull distribution for estimating the parameters of the psychometric function. The psychometric function was fitted with Eq. (1), where P was the proportion of choosing blue at each intensity Δc, k was the slope, and Δc_0 was the point of subjective equality. The equi-bright intensity of blue was calculated by dividing the interquartile range of the function by two: equi-bright = $(\Delta c_{.75} - \Delta c_{.25})/2$.

$$P = \frac{1}{1 + e^{(-k)*(\Delta c - \Delta c_0)}} \quad (1)$$

Results

1. Latency distribution

In the saccade experiment the three saccade paradigms produced a wide range of saccade latency distributions, as illustrated in Figure 1.2. As expected, gap and no gap paradigms produced shorter saccade mean latencies (M ± SD) of 169.5 ± 15.1 ms and 183.1 ± 16.7 ms, respectively, while the overlap paradigm resulted in longer saccade latencies with a mean latency of 238.6 ± 42.8 ms. In the pursuit experiments latencies of pursuit initiation or initial saccades were even longer. In Experiments 1 and 2, the mean latency for pursuit initiation across all observers was 280.9 ± 33.6 ms and 282.8 ± 33.5 ms, respectively, while the mean latency for initial saccades was 373.6 ± 57.2 ms and 387.7 ± 59.2 ms, respectively. To test for significant differences with respect to saccade latencies across the different experimental conditions, we used Friedman's test, a non-parametric alternative to repeated-measures ANOVA. The analysis was conducted on the mean saccade latencies of the subjects, and the results revealed a significant effect of the experimental conditions on saccade latencies ($X^2(2, N = 21) = 40.1, p < 0.001$). Post-hoc pairwise comparisons were conducted using the Wilcoxon signed-rank test with Bonferroni correction for multiple comparisons. Significant differences were found between each paradigm (gap vs no gap: $z = 2.45$, $p = 0.045$, gap vs overlap: $z = 3.62$, $p < 0.001$, no gap vs overlap: $z = 2.89$, $p = 0.012$). These results indicate that the experimental paradigms had a significant and systematic effect on saccade latencies.

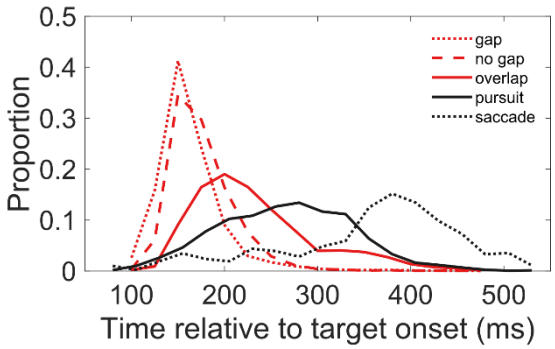


Figure 1.2. Latency distributions of saccades tested with three paradigms in the saccade experiment and of pursuit and initial saccades in the pursuit experiment. The *x*-axis represents the time relative to target onset, while the *y*-axis shows the normalized proportion of trials for all conditions. For the saccade experiment red lines represent latencies for the gap (dotted line), the no-gap (dashed line), and the overlap paradigm (solid line). For Experiment 1 of the pursuit experiment black lines represented the latency of pursuit initiation (solid line) and initial saccade (dotted line).

2. Target selection

We examined the proportion of bluish and yellowish target choices in saccade and pursuit Experiment, as shown in Figure 1.3. In the equi-luminant pair, the proportion of target selection would be close to 50% if both eye movements were determined solely by luminance, whereas there would be more bluish target choices compared to yellowish ones if the eye target choice is determined by heterochromatic brightness. Our results showed that the mean proportion of choosing the bluish stimulus as a target is 48% in the gap paradigm and 53.3% in the no gap paradigm. Here the experimental conditions resulted in shorter saccade latencies suggesting that target selection was guided primarily by luminance information. However, the proportion of eye movements directed to the bluish stimulus increased as latencies lengthened: the bluish stimulus was chosen as a target for saccades in 61.1% of the trials in the overlap paradigm, and in the pursuit experiment as a target in 68.6% of the trials during pursuit initiation and in 65.6% as a target for initial saccades. These results indicate that target selection is more influenced by heterochromatic brightness which was supported by our statistical analysis: one sample t-test with test value at 50%: overlap: $t(20) = 2.77$, $p = 0.012$, Cohen's $d = 0.605$; pursuit: $t(16) = 3.85$, $p < 0.001$, Cohen's $d = 0.933$; initial saccade: $t(16) = 4.10$, $p < 0.001$, Cohen's $d = 0.995$. We also find a significant difference between the choice proportion as targets for saccades produced with the gap and overlap paradigms ($t(20) = 3.82$, $p < 0.001$, Cohen's $d = 0.779$), suggesting that different underlying mechanisms guide saccadic target selection.

For the equi-bright pairs (Figure 1.3B), the bluish stimulus was chosen as a target in the gap, no gap, and overlap paradigm in 35.4%, 31.2%, and 35.6% of the trials. This result indicates that the perceptual equi-bright (Guan et al., 2024) is not consistent with the oculometric equi-bright, as the yellowish stimulus (intensity = 0.15) needs to be dimmer to match the bluish one at 0.485 during saccadic eye movements. In the pursuit task, we had a pair with a yellowish stimulus at an intensity of 0.121 and a bluish one at 0.485 that were close to equi-brightness, with the mean proportion of choosing a bluish one as a target for pursuit initiation in 52.8% and for initial saccades in 54.8% of the trials. However, these pairs were not subjectively equi-bright to all individual observers.

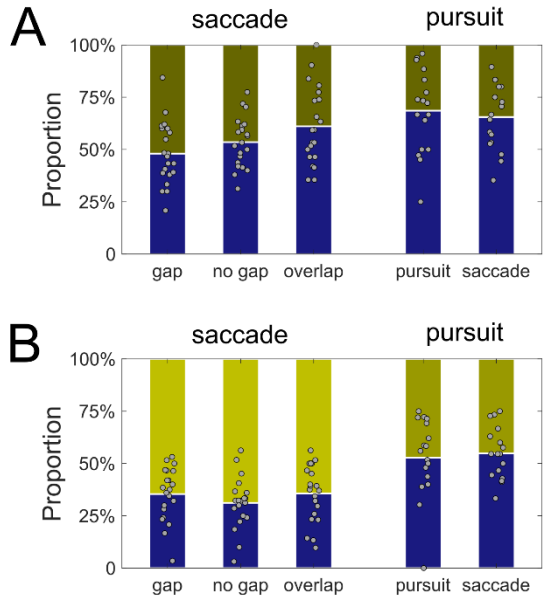


Figure. 1.3. Proportions of choices for blue and yellow stimuli in the equi-luminant (A) and equi-bright (B) pairs. The dividing line between the yellow and blue sections in each bar represents the mean proportion of each choice, with the yellow section at the top and the blue section at the bottom. Each dot represents an individual observer. For equi-luminant pairs, the blue choices increase as the latency increases. For equi-bright pairs, the blue stimulus has the same intensity in all four paradigms, while the yellow stimulus has a lower intensity in the pursuit paradigm (intensity = 0.121) compared to the other three saccade paradigms (intensity = 0.15). Here, the blue choices increase as the latency increases.

3. Target selection according to latency

Since the processing of chromatic signals is delayed compared to luminance signals (Kaplan & Shapley, 1982; Maunsell et al., 1999; Maunsell & Gibson, 1992), we checked whether their color choices differ with respect to eye movement latencies. Specifically, in the saccade experiment, we pooled the latencies of valid saccades of all observers across the three saccade paradigms and divided them into predefined latency intervals in steps of 50 ms. For the pursuit experiment, we merged pursuit trials with latencies longer than 200 ms and shorter than 350 ms and divided them into intervals in steps of 50 ms. Due to the normal distribution of latencies, the number of trials per interval varied; to address this, we used bootstrapping (1,000 resamples) to estimate 95% confidence intervals for the proportions. This was done separately for the equi-luminant and equi-bright pairs, as shown in Figure 1.4. In both experiments, the proportion of bluish target choices as targets for saccades or pursuit eye movements increased as the latency increased. This result found for the initiation of both saccade and pursuit suggests that short-latency eye movements are driven mainly by luminance, while long-latency eye movements are more guided by heterochromatic brightness.

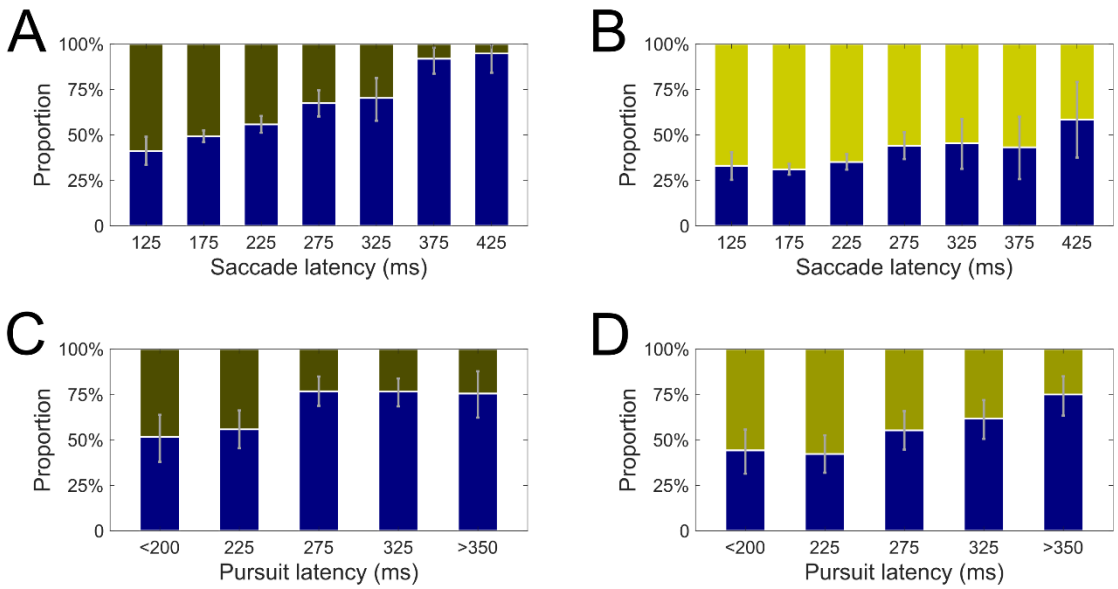


Figure 1.4. Proportions of target choices between bluish and yellowish stimulus pairs for latency interval of 50 ms of the saccade (A and B) and pursuit (C and D) experiment. The dividing lines between the yellowish (top) and bluish (bottom) sections in each bar represent the mean proportions of target choices; the gray vertical lines denote the 95% confidence intervals of the mean bluish target proportion. *A* and *C* show the results for equi-luminant stimulus pairs, while *B* and *D* show the results for equi-bright pairs. Numbers along the *x*-axis represent the center of each latency bin width; for example, 125 indicates a latency range from 100 to 149 ms.

4. Weights of equi-bright yellowish and bluish stimuli during pursuit initiation compared to perception

To identify the weight of equi-bright yellowish and bluish stimuli during pursuit initiation, we fitted a psychometric function to the color choices of our participants to determine the PSE in oculometric brightness. Eight observers were excluded since the slopes of the fitting curve to their data were lower than 1. We found that a bluish stimulus at an intensity of 0.278 (4.2 cd/m^2) approximately matched the yellowish one at an intensity of 0.05 as shown in Figure 1.5. In the heterochromatic brightness ranking experiment (see above), the max-weighted RGB model has been shown to be the best predictor of heterochromatic brightness, with the optimal RGB weights at [0.40, 0.45, 0.15] (Guan et al., 2024). According to these weights, a bluish stimulus at an intensity of 0.162 reaches perceptual equi-brightness to a yellowish stimulus at 0.05. Thus, for pursuit initiation, the oculometrically equi-bright bluish stimulus exhibited a weaker influence compared to the perceptually equi-bright stimulus of the ranking task. Given the difference between the two tasks, this difference is not surprising.

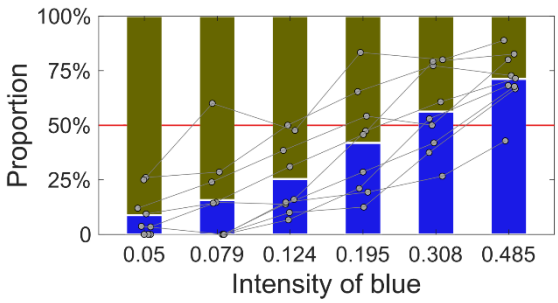


Figure 1.5. A. Proportions of choices between bluish and yellowish stimuli. The dividing line between the bluish (bottom) and yellowish (top) sections of each bar represents the mean proportion of target choices. Each dot indicates an individual observer. The horizontal red line shows the percentage of 50%.

S-cone control

We conducted additional control experiments for both, the pursuit and saccade experiments. Our bluish and yellowish stimuli differ dramatically in their S-cone excitation. The bluish stimulus has nearly 100 times higher S-cone activation than the yellowish stimulus of the same luminance. However, since the L- and M-cone excitations of bluish and yellowish stimuli in our experiment were not identical, one may question whether the dominance of bluish target choices can be solely attributed to the contribution from S-cones. In this control experiment, we therefore created a stimulus that had identical L- and M-cone excitations as the previous yellowish stimulus but differed only in S-cone excitation. This led to a purplish-looking stimulus. We also used equi-luminant yellowish and bluish pairs that were made equi-luminant using the CIE luminous efficiency function derived from the Stockman & Sharpe cone fundamentals (Sharpe et al., 2005; Stockman et al., 2008).

In the control saccade experiment mean latencies (M ± SD) for the gap, no gap, and overlap paradigm were 189.7 ± 20.5 ms, 197.3 ± 19.9 ms, and 258.4 ± 31.7 ms. In the pursuit control experiment mean latencies of pursuit initiation and initial saccades were 299.9 ± 36.7 ms and 416.5 ± 46.6 ms, respectively. For all conditions, the proportion of choices when the bluish target was the CIE XYZ 2015 or the S-cone isolating stimulus was either the same or higher than for the original stimulus (Figure 1.6). This result indicates that the major driver for bluish choices in all paradigms was indeed caused by a stronger S-cone contribution.

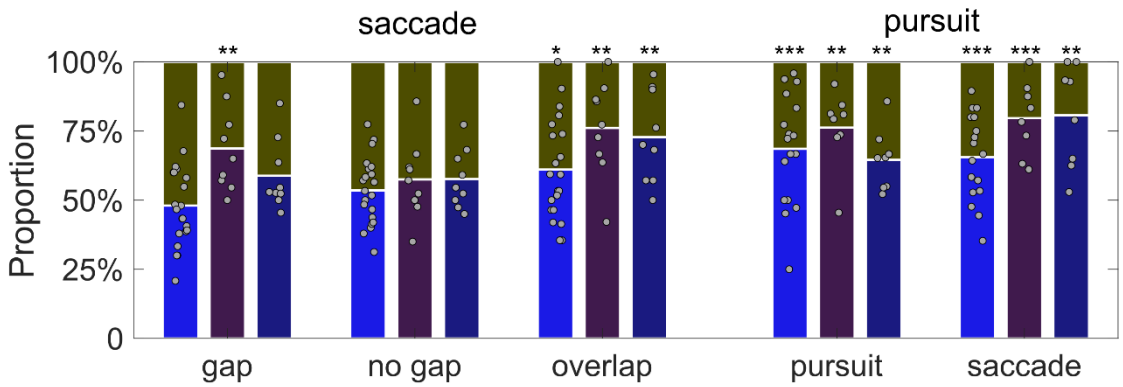


Figure 1.6. Proportions of target choices between yellowish, bluish, and purplish stimuli in the control saccade and pursuit experiments. For each group of three bars, the first bar represents the equi-luminant pair based on CIE 1931, the second bar represents the S-cone isolated pair, and the third bar represents the equi-luminant pair based on the Stockman & Sharpe cone fundamentals (Sharpe et al., 2005; Stockman et al., 2008). The dividing line between the yellowish (top) and bluish or purplish (bottom) sections of each bar represents the mean proportion of each target choice. Each dot represents an individual observer. Asterisks above the bar denote the significance of the difference between the choice proportions compared to 50%, established using one-sample t-tests: * for $p < 0.05$, ** for $p < 0.01$, *** for $p < 0.001$.

Discussion

We studied the effects of luminance and heterochromatic brightness on target directed oculomotor behavior by presenting two competing equi-luminant or equi-bright stimulus pairs in a variety of yellowish, bluish, and purplish colors. Our aim was to measure whether and when target selection processes of the saccade and pursuit system are influenced by the contribution of S-cones. We used different saccade paradigms and stimulus combinations to answer these questions. The results of our different experiments show that for both saccades and pursuit movements the selection between nominally equi-luminant yellowish, bluish, and purplish stimuli is strongly determined by latency. The selection process of short-latency saccades primarily follows luminance, since when bluish and yellowish stimuli matched in luminance they were approximately equally selected as targets by these saccades. However, with increasing saccade latencies proportions of choosing bluish stimuli as targets rose. For longer-latency saccades and smooth pursuit initiations, target selection processes seemed more determined by heterochromatic brightness and resulted in a larger proportion of bluish target choices. Although our stimuli were not tailored to individually isolate S-cone mechanisms in the main and control experiments, we found that the bluish and purplish targets activated the S-cone mechanisms more than the yellowish targets by orders of magnitudes. We therefore conclude that the S-cones contribute to the target selection processes of saccadic and pursuit eye movements especially when their initiations happen after longer latencies.

Our work extends the findings of Baker & Mollon (1993), who showed that luminance mainly determines whether a particular stimulus was chosen over another one. By using different paradigms, we can demonstrate that the target choices for eye movements differ depending on the latency. The target selection of saccades and pursuit movements initiated after longer latencies is significantly influenced by heterochromatic brightness and an increase in S-cone input. Previous behavioral studies have shown that saccadic target selection is partly driven by visual saliency (for review, see (Einhäuser & König, 2010; Itti & Koch, 2001; Kümmerer & Bethge, 2023; Schütz et al., 2011; Tatler et al., 2011)). In our task, saliency is based on the bottom-up characteristics that make one of the two stimuli stand out more than the other. We instructed our observers to select and make an eye movement to the stimulus that appeared more salient. If selection processes for an eye target follow the visual input of luminance only, then the saliency of isoluminant bluish and yellowish stimuli should be equal. However, if S-cone input is involved in target selection, then the bluish stimulus would be more conspicuous

than the yellowish stimulus and should be selected more often. For the yellowish and bluish stimulus pairs, the heterochromatic brightness of blue appeared to be much brighter than that of the yellow when they were equi-luminant. This perceptual difference is due to the lack of the S-cone contribution to luminance (Ayama & Ikeda, 1998; Corney et al., 2009). Our results indicate that the effectiveness of our stimuli to attract and to be selected as a target for saccades and pursuit depends on the latency of these eye movements. Short-latency saccades are primarily determined by luminance, whereas long-latency saccades and pursuits are mainly driven by heterochromatic brightness. Therefore, the target selection switched from yellowish targets for short-latency saccades to more bluish targets for long-latency saccades. This result reflects the dynamics of the S-cone contribution since signals from S-cones take longer to arrive at the neuronal structures that underlie the decision-making processes, presumably the SC (White et al., 2009). A similar dynamic modulation of saccadic target selection was observed by Schütz et al. (2012). They found that short-latency saccades were determined by visual contrast alone, while long-latency saccades also took reward into account (Schütz et al., 2012).

In our experiments we used the CIE V(λ) function (CIE, 1926) and the V(λ) function based on the Stockman & Sharpe cone fundamentals (Sharpe et al., 2005; Stockman et al., 2008). We did not try to evaluate individual differences and optical factors that might influence the distribution of cone excitations across the retina and cause systematic deviations from these functions. We feel that this is not necessary, since our results show massive changes in eye movement behavior at different latencies – while the stimuli stay identical. Of course, such factors would affect absolute choice proportions, but they would not affect selection changes with latency. The macular pigment, for example, would be expected to influence target selection with respect to eccentricity. In the central 1-2 degrees, where most flicker photometric measurements for defining luminance were made, S-cones are massively attenuated by macular pigmentation (Bone & Landrum, 2004). We used the ISETBio software (Cottaris et al., 2019) to estimate these effects. At 4 degrees, where we presented our two stimuli, macular pigment density is much lower, leading to a relative attenuation of the luminance for the yellowish targets by about 20% compared to the bluish and purplish targets. For the pursuit experiment, the macular pigmentation is less relevant since both stimuli appeared first at an eccentricity of 1.5 degrees and moved towards the fovea.

By employing three paradigms (i.e., gap, no gap, and overlap) in the saccade experiment, we induced saccades with different mean latencies: around 190 ms with the gap and no gap and around 250 ms with the overlap paradigm. This wide latency distribution allowed us to

investigate how the timing of eye movement initiation affects target selection for bluish and yellowish stimuli at different intensities. This effect became particularly evident when analyzing target selection in trials with equi-luminant stimulus pairs using finer latency bins. Starting from the fastest saccades (100–150 ms) to the slower ones (>400 ms), we observed a progressive increase in the selection of the bluish target. Notably, pursuit initiation in our experiment happened after a relatively long latency (~280 ms across all observers) and compared to experiments with a single-target pursuit task (Rashbass, 1961). In our experiments, pursuit onsets are also slower than saccade onsets (see Figure 1.2). This might be due to several reasons. Firstly, we used always two competing stimuli, which required additional time for target selection processes before an eye movement could be initialized. In previous eye movement studies involving competing stimuli, pursuit onset latency ranged from 100 to 400 ms (Liston & Krauzlis, 2005; Spering et al., 2008), which is consistent with the latencies observed for pursuit in our experiments. Secondly, some of our stimuli had low intensity. Previous studies have shown that the latency of both, smooth pursuit and saccadic eye movements increases when stimulus contrast decreases (D. I. Braun et al., 2008; Goettker et al., 2019; Spering et al., 2005). Therefore, the use of dim stimuli in our experiments has most likely contributed to longer latencies for the initiation of eye movement. Similar to the gap effect on saccade latencies, pursuit onset latency is reduced when the gap paradigm is used for a pursuit task (Knox, 1996, 1998; Krauzlis & Miles, 1996).

Taken together our results extend earlier findings especially of Baker & Mollon (Mark. R. Baker & Mollon, 1993) because they make clear that target choices for eye movements differ depending on their latencies. The influence of heterochromatic brightness and S-cone input increases with latencies. Our results are in line with the important role color plays when viewing or searching natural scenes (Amano & Foster, 2014; Frey et al., 2008; Nuthmann & Malcolm, 2016).

III. Color discrimination in action: High-throughput measurement in immersive VR

Introduction

Color discrimination is a fundamental aspect of human visual perception. Our ability to differentiate between subtly distinct colors is crucial for tasks ranging from object recognition to aesthetic appreciation. Color discrimination has been studied early and extensively, using both modelling (Danilova & Mollon, 2012, 2014; Krauskopf & Gegenfurtner, 1992; MacAdam, 1942; Rinner & Gegenfurtner, 2000; Schrödinger, 1920; Stiles, 1959; Von Helmholtz, 1867; Wright, 1941; Wyszecki & Fielder, 1971), providing insights into the mechanisms underlying color vision. Color matching has been widely applied to quantify color discrimination thresholds (W. R. J. Brown & MacAdam, 1949; MacAdam, 1942), used to then determine discrimination contours on a plane of color space. Similarly, these contours can be determined with odd-one-out tasks (Krauskopf & Gegenfurtner, 1992; Rinner & Gegenfurtner, 2000; Hedjar et al., 2025b, 2025a; Hansen et al., 2008). In addition, the CIEDE2000 color-difference formula is an industry standard for determining color differences (Luo et al., 2001, 2023; Fairchild, 2013; Sharma et al., 2005; Gao et al., 2023; CIE-Commission & others, 1976). It is derived from empirical discrimination datasets and perceptual adjustments intended to improve uniformity. However, most of this color discrimination literature is based on limited psychophysical data, collected from few observers, who were highly restrained in their movements while judging very simple stimuli such as uniform discs or patches. We try to remedy this situation by exploring ways to make large-scale data collection more feasible.

The difficulty of measuring the full metric of color space is best illustrated by the enormous effort David MacAdam (MacAdam, 1942) undertook to determine the seminal discrimination ellipses that bear his name. These remain the most complete dataset available, even though thresholds were measured only in a single plane of color space. Later, MacAdam and Brown (W. R. J. Brown & MacAdam, 1949) and Wyszecki and Fielder (Wyszecki & Fielder, 1971) extended the work to three-dimensional discrimination ellipsoids, still limited to the same chromaticity centers. The study of Brown and MacAdam (W. R. J. Brown & MacAdam, 1949) required about 48,000 individual settings over 18 months of testing by a single observer.

Clearly, extending this approach to the entire three-dimensional color space is not feasible. The space is vast, sensitivity varies with direction and location, and the number of required measurements grows exponentially with dimensionality—a classic example of the "curse of dimensionality" (Bellman, 1957). As a result, no comprehensive dataset exists that maps discrimination thresholds across the full color space.

What can be done then? One approach is to increase data throughput by using new paradigms that allow faster sequences of judgements and are less tiring for the observer. A different approach tries to get away with fewer data points through interpolation or global fitting. Here we pursue the first approach by embedding data collection within an interactive VR game that participants play for extended periods of time. In the game, as in the real world, perceptual judgements are embedded within action and interaction. The alternative approach was recently demonstrated by Brainard et al. (Hong et al., 2025), who used advanced fitting methods and interpolation to reconstruct a complete metric field, but still within a single plane of color space. In principle, the two approaches are complementary and could ultimately be combined.

Our approach also addresses broader questions about the generalizability of laboratory psychophysics. While psychophysical methods have been the cornerstone of perceptual science, there have been recent concerns about the generalizability of data collected under controlled lab conditions to "real-world" perception (Aanstoos, 1991; Kingstone et al., 2008; Osborne-Crowley, 2020; Shamay-Tsoory & Mendelsohn, 2019). Discrepancies in perceptual estimates from psychophysical lab studies may arise for several reasons. Firstly, attentional lapses from observers over prolonged and boring experiments may introduce additional variability in perceptual thresholds. Secondly, visual stimuli in the real world can be complex and feature rich. Simplifying and isolating the cues present in stimuli may elicit biased responses due to perceptual priors that have evolved for natural vision (Yildirim et al., 2021). Finally, perception is typically embedded within action. Sensory processing is shaped by our goals, movements and expectations. It has been shown in animal studies that locomotion is often associated with improved perceptual behaviour such as visual detection (Bennett et al., 2013). This effect seems to be caused by a boosted response gain (Niell & Stryker, 2010), and improvement encoding of visual stimuli in the visual cortex (Dadarlat & Stryker, 2017). It is therefore important to explore perception under more active conditions.

We therefore measured color discrimination thresholds in an immersive, action-based task. While absolute thresholds are likely to vary depending on experimental factors such as the adaptation point and stimuli presentation timings, we expected to replicate several key findings in the color discrimination literature. Previous research consistently reports that color

discrimination sensitivity is not-uniform across modern color spaces. Early measurements by MacAdam (MacAdam, 1942) revealed elliptical discrimination contours in CIE 1931 chromaticity space. In Munsell color space, Judd demonstrated that chroma JNDs were approximately twice as large as hue differences, a phenomenon he described as the "super-importance of hue" (Judd, 1941). Subsequent work confirmed that thresholds are typically higher for chroma than for hue (Danilova & Mollon, 2014, 2016) in both the DKL (Derrington et al., 1984; Hedjar et al., 2025b, 2025a) and MacLeod-Boynton (MacLeod & Boynton, 1979) color spaces. Furthermore, the difference between hue and chroma thresholds is not uniform throughout color space. Purplish and greenish colors tend to produce smaller chroma-to-hue threshold ratios, while they are greater for bluish and orangish colors (Hedjar et al., 2025a). The central question here was whether these canonical asymmetries would be preserved under immersive, motor-engaged conditions.

Main Experiment

To address this question, we embedded a standard 4-AFC odd-one-out color discrimination paradigm within an immersive virtual reality (VR) environment inspired by the rhythm game *Beat Saber*. A similar approach was recently used by Aizenman et al. to measure color category boundaries (Aizenman et al., 2024); here, we extend this methodology to quantify color discrimination thresholds. On each trial, four color patches were presented on the front face of an approaching cube. Three patches shared a reference color, and one was a target differing in either hue or chroma. Participants indicated the location of the odd-one-out target by slicing the cube in the corresponding direction.

Methods

The task retained the interactive dynamics of *Beat Saber*, in which players slice musically synchronized cubes using handheld controllers, but replaced the original directional arrow cues with chromatic discrimination judgments. By systematically varying the chromatic difference between reference and target using a method-of-constant-stimuli procedure, we estimated hue and chroma discrimination thresholds.

A. Participants

A total of 24 participants (15 females, average age = 29.8, range 23-38 years) took part of the first experiment. Two participants had to be excluded because they didn't follow the task instructions correctly. All participants had normal or corrected-to-normal eyesight and normal color vision, as tested by the 24-plate edition of Ishihara plates (Clark, 1924). Before the experiment participants were informed about the procedures and signed written consent forms. This study was approved by the ethics commission of the Department of Psychology at Justus-Liebig-Universität Giessen (LEK 2020-0015).

B. Apparatus

We developed our 'BeatSaber' clone using Unity (version 6000.0.22f1). The game was built for an Android build target to run locally on Meta Quest headsets and made use of the Meta XR Core, Interaction and Haptics SDKs (version 76.0). For our experiment, we presented the game on a Meta Quest 3 headset (90 Hz refresh rate, LCD display, resolution of 2064 x 2208 pixels per eye). The display was color calibrated by a CS-2000A spectroradiometer (Konica Minolta, Chiyoda, Tokyo, Japan), with calibration stimulus control being implemented in Unity

and MATLAB, as in the prior work Díaz Barrancas et al. (Díaz-Barrancas et al., 2024; Díaz–Barrancas et al., 2023). The red, green, and blue primaries of the display had CIE x, y, Y coordinates of [0.649, 0.327, 98.337], [0.299, 0.606, 346.140], and [0.151,0.058, 35.606], respectively.

Color discrimination thresholds were measured across eight conditions defined by two reference colors (purple-ish and orange-ish), two stimulus dimensions (hue and chroma), and two shift directions for each dimension: toward or away from the grey adaptation point for chroma, and clockwise or anticlockwise angular shifts for hue (see Figure 2.1).

We specified chromaticities in Derrington–Krauskopf–Lennie (DKL) (Derrington et al., 1984) color space and we used conventions detailed in Hansen and Gegenfurtner (2013) to define the DKL axes and to compute the transformation from DKL to device RGB values (Hansen & Gegenfurtner, 2013).

C. Stimuli and Procedure

The two reference colors lay on radial lines on the isoluminant plane, one at 45° (Quadrant 1, purple-ish) and the other at 315° (Quadrant 4, orangish). The reference colors lied 0.17 DKL units from the origin. For each discrimination dimension and direction, we computed 10 shifts between 0 and 0.07 DKL units away from the two reference points.

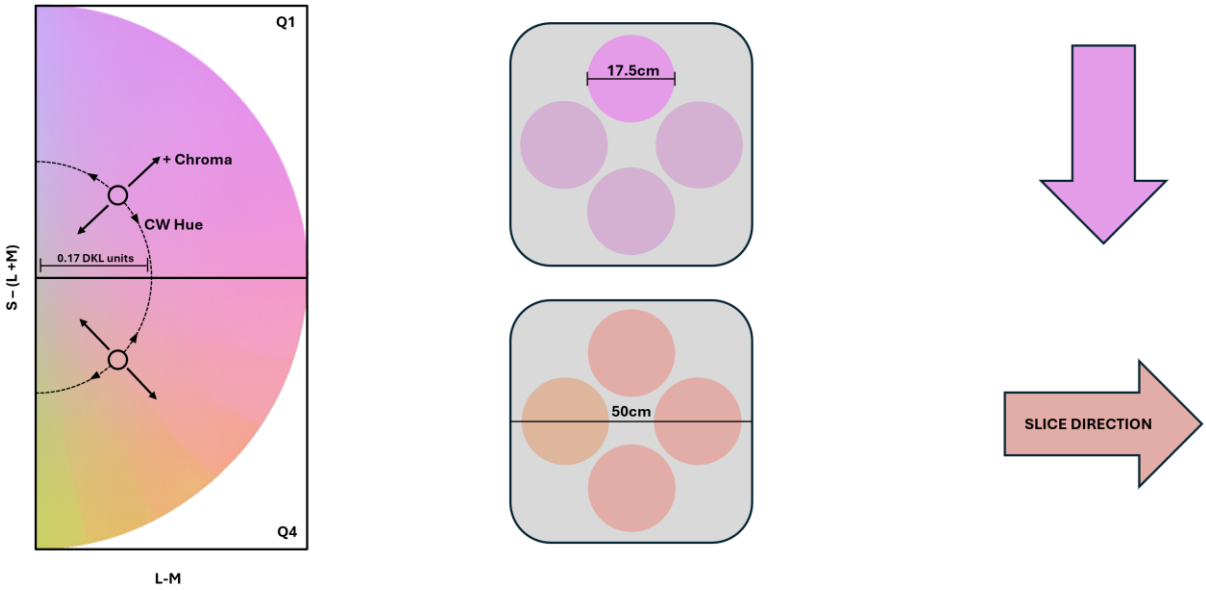


Figure 2.1. (a) Reference stimuli (black circles) and the directions along which discrimination was measured in DKL space. Solid black arrows represent shifts in chroma, with towards the central grey point being a negative shift, and away a positive shift. Dashed arrows represent hue shifts, either clockwise or anticlockwise. We calculated 10 even steps along each shift direction for estimating threshold via method of constant stimuli (b) Representation of the stimuli on the cube frontal face. Three patches were the reference color and one odd-one-out was a different color. Participants were required to slice through the cube starting from the side which contained the odd-one-out patch.

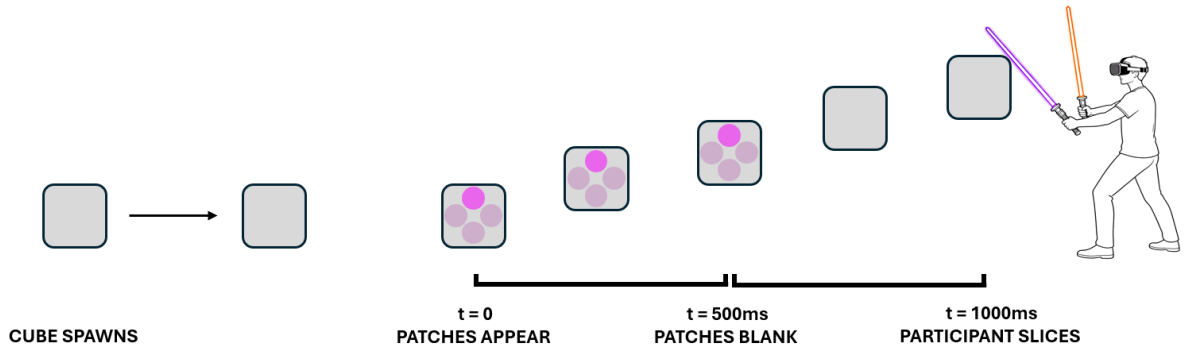
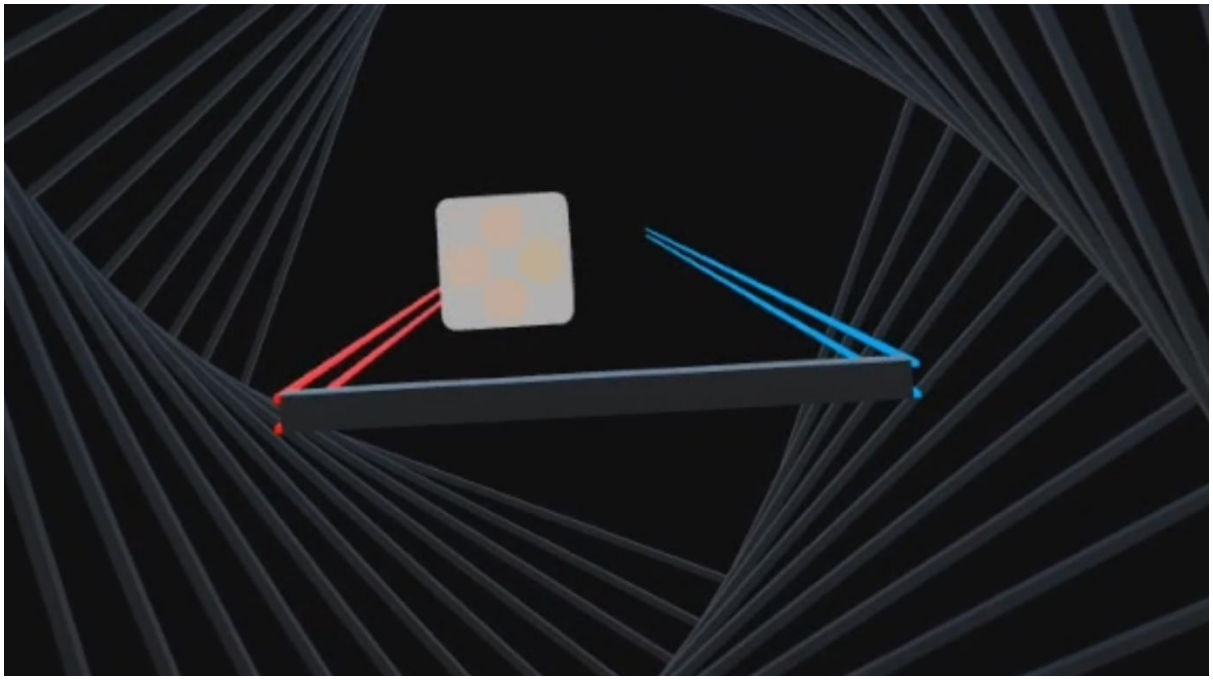


Figure 2.2. Example progression of a single cube during a trial.

Figure 2.2 shows the progression of a single cube during a trial (see also Movie 1). Each trial consisted of participants slicing a cube moving towards them which had contained four color patches on the front face. Three patches were the reference color and one odd-one-out was a shifted color. The cube used an unlit material set to the isoluminant midgrey color. Cube faces were approximately 50cm in width and height, and each patch was 17.5cm in diameter. During the stimulus presentation range, this meant that patches subtended approximately 1 – 2 degrees retinally. Each cube was generated at a fixed distance of 40m from the participant's viewpoint and moved along a predefined trajectory that ended with a final "bounce" towards the player.

We defined a trial as the 1-second interval from the onset of the bounce to the moment the participant slashed it. In the first 500ms of this interval, the block displayed the stimuli. After this, mid bounce, the cube's face turned blank. The cube continued its trajectory towards the participant for another 500ms where it could then be sliced. Participants heard a feedback sound upon slicing the cube.



Movie 1. A participant playing the BeatSaber game. See uploaded movie file.

Blocks of trials were organized into 2.5-minute soundtracks. Figure 2.3 shows an example stream of trials within a single soundtrack. Each soundtrack contained 100 trials split between two conditions in separate left and right cube streams. Each stream contained 50 cubes, 5 repetitions of each of the 10 target patch intensities. The soundtracks were all 160 beats per minute, with cubes synchronized to appear on every 4th beat, resulting in 40 trials per minute.

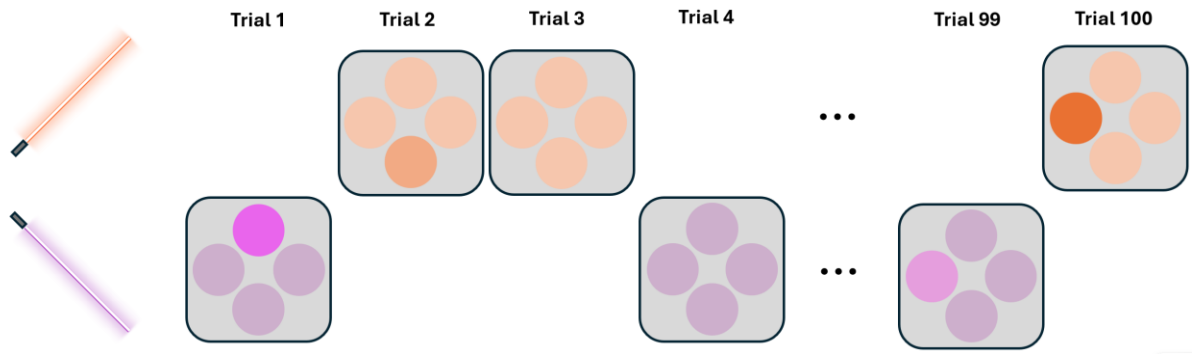


Figure 2.3. Example stream of cubes (trials) in a block. Each block contained 100 trials. Color conditions were split into left and right streams, 50 on either side.

Prior to the main experiment, participants completed a short training session to gain familiarity

with the task. The training session required participants to complete soundtracks in which the target patch was highly different to the reference. They played until they achieved a hit rate of 97% or above. For the main experiment, we separated the 8 conditions into 4 soundtracks, each containing an orange-ish and purple-ish stream and with target patch shifts being either in hue clockwise, hue anti-clockwise, chroma positive, or chroma negative. Participants completed each soundtrack 3 times, resulting in 15 repetitions per stimulus intensity level for all 8 conditions.

Finally, to ensure that the 'BeatSaber' methodology did not produce unwanted discomfort or sickness for participants, they completed the Simulator Sickness Questionnaire (Kennedy et al., 1993) at the end of the experiment.

Results and Discussion

We fitted psychometric functions to the individual data using the psignifit toolbox for MATLAB (Schütt et al., 2016; Wichmann & Hill, 2001). The lower limit of the function was 25% correct (chance level for 4AFC) and the upper limit was 100% correct, so we defined discrimination thresholds at 62.5% correct. Figure 2.4 shows exemplary psychometric function fits. Figure 2.5 shows the color discrimination thresholds for the purple-ish and orange-ish quadrant on the equiluminant plane of DKL. We averaged thresholds across both directions within each color dimension (i.e., increasing and decreasing for chroma and clockwise and counterclockwise for hue). We found that a linear mixed-effects model best fit our data, determined by comparing Akaike Information Criterion (AIC), using color dimension and quadrant as fixed effects factors with their interaction specified. Participant was set as a random-effects factor with varying intercepts. To meet model assumption, threshold in DKL units were transformed in *log* units as the dependent variable. We applied a two-way ANOVA to this model, with fixed effects of quadrant and color dimension and their interaction.

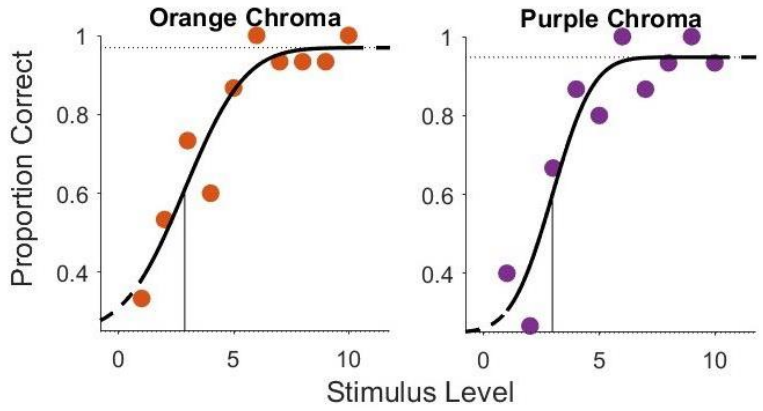


Figure 2.4: Exemplary individual psychometric curve fits for orange (left) and purple (right), for a single direction. The x-axis represents stimulus intensity in discrete steps along the DKL color space, measured relative to the reference color (1 = closest to the reference; 10 = farthest). The y-axis represents the proportion of correct target selection. The colored circles represent observed data for each condition, and solid black curves show the fitted cumulative Gaussian psychometric functions. The vertical gray lines indicate the estimated discrimination thresholds (62.5% correct). Dashed horizontal lines mark the lower and upper asymptote of the fitted functions.

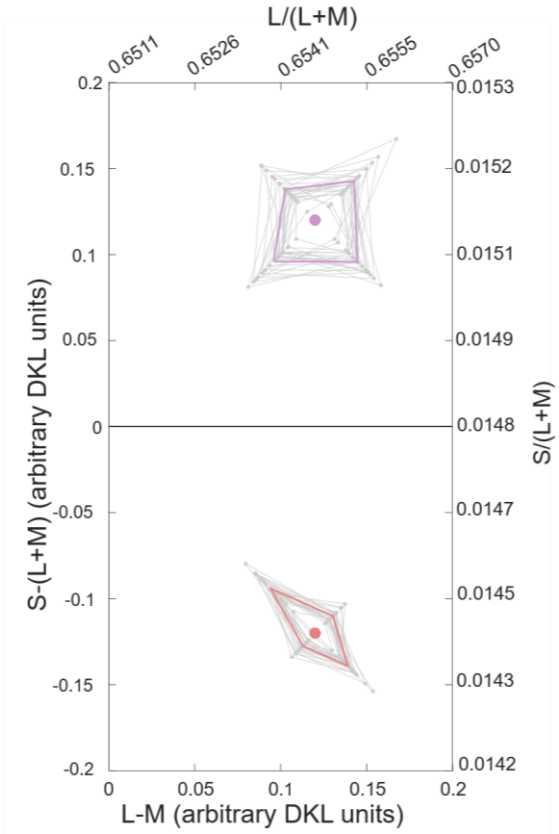


Figure 2.5. Individual discrimination thresholds for all participants shown in DKL color space. The *x* and *y* axis are defined by arbitrary DKL units. The two reference points as dots color-coded by quadrant color. Mean thresholds are outlined with colored lines around each reference point, while individual participant thresholds are connected by grey lines. The upper and right side of the axis display MacLeod-Boynton coordinates (MacLeod & Boynton, 1979)

Figure 2.6 shows the average and individual thresholds for all conditions. Our data aligns with the results from previous work on color discrimination (Hedjar et al., 2025a, 2025b; MacAdam, 1942), namely that chroma thresholds were typically larger than hue thresholds. We found a main effect of color dimension, with chroma thresholds being significantly larger than hue thresholds ($F(1,56) = 154.4$, $p < 0.001$). Further, this difference between chroma and hue thresholds was not uniform throughout color space. There was a significant interaction between quadrant and color dimension ($F(1,56) = 61.1$, $p < 0.001$). In the orange quadrant, hue thresholds were smaller than chroma, while this difference was not significant in the purple quadrant ($F(1,56) = 0.94$, $p = 0.33$). No main effect of quadrant was observed.

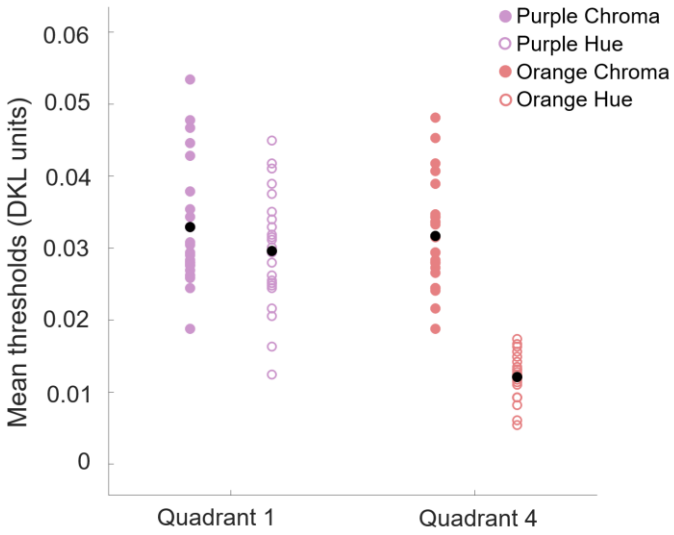


Figure 2.6: Mean and individual detection thresholds, expressed as Euclidean distance from the reference points in DKL space. The thresholds are collapsed across chroma and hue dimensions and displayed for Quadrant 1 (purple) and Quadrant 4 (orange). Each participant's threshold is represented by a colored dot (filled for chroma, open for hue) and the group average is indicated by a black dot.

Our study replicated well established color discrimination phenomena, namely, that chroma thresholds are larger than hue thresholds, and that this difference varies across color space. In the orange-ish region of DKL color space, the difference between chroma and hue thresholds is much larger than the purple-ish region. Our findings provide further evidence for the "super-importance of hue" (Danilova & Mollon, 2016) and suggest that this effect is robust even under more active, embodied task conditions.

To assess whether VR-related discomfort might have influenced participant performance, we administered the Simulator Sickness Questionnaire (SSQ) at the end of the experimental

session. This questionnaire evaluates the physical and mental state and its score ranges from 0 to 235.6 (Kennedy et al., 1993). The SSQ score had an average of 21.14 ± 19.99. In comparison, the meta-analysis by Saredakis et al. (Saredakis et al., 2020) on visually induced motion sickness reported a higher average of 27.4 ± 3.1 for experiments of similar length. Further, no participant verbally reported feeling sickness or discomfort during the experiment. These results suggest that the head-mounted display (HMD) and immersive VR experimental design did not elicit significant visual discomfort during the study.

A key contribution of our study lies in embedding psychophysical measurement within an engaging, game-based structure. Gamified paradigms have been shown to enhance participant motivation, enjoyment, and sustained attention during perceptual and cognitive tasks (Hamari et al., 2014; Lumsden et al., 2016; Mekler et al., 2017). For psychophysics, such factors are not merely experiential but methodological: reduced boredom and attentional lapses may stabilize performance across extended testing sessions and improve effective data yield. In the present task, minimal training was required, and participants were able to sustain a high trial rate while maintaining stable psychometric performance.

While these results demonstrate that color discrimination can be effectively assessed in an immersive, game-based context, it remains important to ensure that this paradigm does not compromise data quality or introduce bias. To address this, we conducted a follow-up control experiment designed to directly compare the reliability of the 'BeatSaber' method with a more traditional keyboard-response task, and to quantitatively compare participant enjoyment between these two tasks.

Control experiment

We designed two additional control conditions in order to properly assess participant enjoyment and the data quality of our 'BeatSaber' method. Our first control (Control Key-Press) aimed to isolate any potential effects of the dynamic slicing participant response method on the quality of psychophysical measurements. We kept visual stimuli and timing exactly the same as in the 'BeatSaber' version, but participants instead had to indicate the direction of the odd-one-out target via keyboard arrow input. This task, however, was still quite fun as it involved moving cubes. To assess enjoyment of the 'BeatSaber' method we designed a further experiment (Control Classic) which more closely resembled a traditional psychophysical color discrimination experiment. In this version participants responded with arrows keys to further simplified stimuli, consisting of centrally located color patches on a full screen uniform grey background. There was no music during this version.

Methods

10 participants from the main experiment returned to participate in our controls. In one session we measured color discrimination thresholds using the 'BeatSaber' method, Control Key-Press, and Control Classic. The order of the experimental conditions was counterbalanced across participants.

For simplicity we measured thresholds for only one direction of each dimension (chroma and hue) of the same reference colors (purple-ish and orange-ish). We measured thresholds in the descending chroma direction and counterclockwise direction for hue. For each experimental condition (Beat Saber, Control Key-Press, Control Classic) we collected 600 trials, so that we would have the same number of repetitions as in the main experiment.

In Control Key-Press we simply changed the input method from slicing the cubes with controllers to a keyboard arrow press. When the cube reached the point that the participant would need to slice, it waited for the participant to respond with a direction. In Control Classic, a static centered stimulus was presented against a uniform grey background. The presentation time was matched to the duration of Beat Saber and Control Key-Press trials (500ms) and the stimulus size matched the disks at the end of the bounce phase (approximately 2 degrees). No music was played for this condition, and responses were given via key press, with only feedback sounds provided.

After completing each condition, participants filled out the Intrinsic Motivation Inventory (Ryan et al., 1983) and the User Experience Questionnaire (Laugwitz et al., 2008), which was

adapted to refer to the experimental conditions by replacing the term 'product' with 'experiment'.

Results and Discussion

We first assessed the quality of the data collected across the three conditions – Beat Saber, Control Key-Press and Control Classic. To assess the goodness of fit, we calculated the deviance of the data from the fit and compared it with the distribution of deviances that would be observed where the fit is the true psychometric function. For the 10 participants, using 2 color reference points and 2 measurement directions (descending chroma and hue), a total of 40 psychometric fits were obtained, resulting in 40 deviance values. For Beat Saber, 4 fits (10%) were rejected at the 5% significance level. In Control Key-Press, only 1 fit (2%) was rejected, while in Control Classic, 4 fits (10%) were rejected at the same significance threshold. The rejection rates observed are consistent with those typically reported in psychophysical research. (Jäkel & Wichmann, 2006). This suggests that the chosen psychometric model adequately described the data across all conditions, with only minor deviations that are likely to reflect transient changes in observer performance rather than systematic error.

We compared thresholds from the Beat Saber task and Control Key-Press, where the key difference was simply the input method (swiping with the controllers versus keyboard press). Figure 2.7 shows individual and mean chroma and hue thresholds for both BeatSaber and Control Key-Press conditions. Overall, no significant differences, assessed with paired t-tests, were observed between Beat Saber and Control Key-Press, except for chroma in the purple-ish quadrant ($t(9) = 2.453$, $p = 0.036$, Cohen's $d = 0.775$).

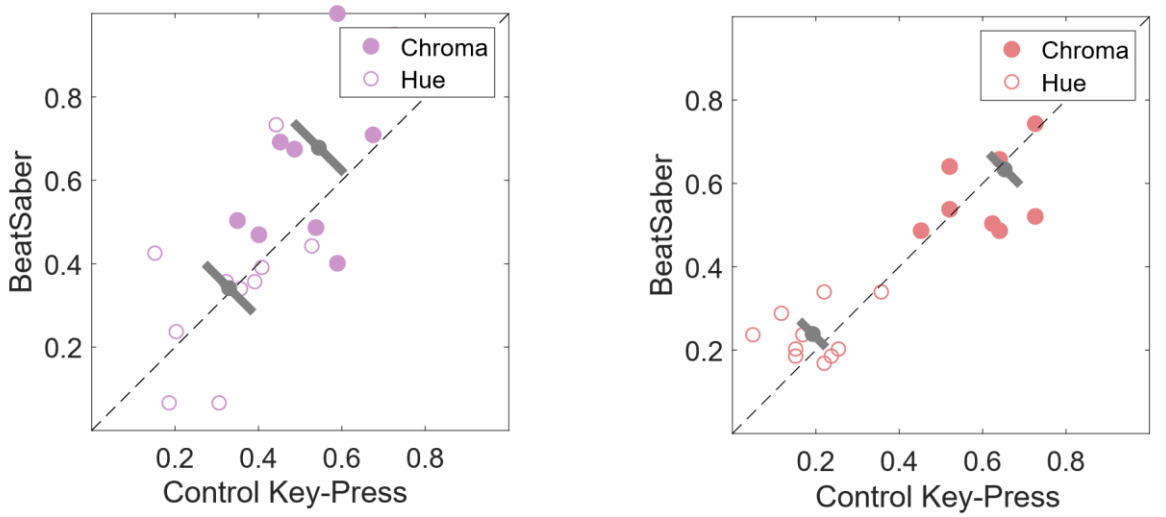


Figure 2.7. Discrimination thresholds for chroma and hue for the Beat Saber and Control Key-Press conditions. Axes show discrimination thresholds in terms of discrete stimulus intensity levels, normalized between 0 and 1. Left panel purple color quadrant; right panel orange color quadrant. Filled dots represent chroma thresholds, open dots represent hue thresholds for individual participants. Grey diagonal bars, one for chroma and one for hue, represent the group mean difference and its 95% confidence interval.

Finally, we compared the scores from the Intrinsic Motivation Inventory and the User Experience Questionnaire between the Beat Saber and Control Classic conditions. Due to fundamental differences between these paradigms – moving versus static stimuli, different backgrounds therefore different adaptation state – we did not directly compare the thresholds across these conditions.

Figure 2.8 shows the mean IMI scores for the 'Enjoyment' and 'Pressure' subscales, and Figure 2.9 shows the UEQ scores. The IMI scores reveal that participants found Beat Saber significantly more enjoyable compared to Control Classic ($t(9) = 4.07$, $p = 0.002$, Cohen's d = 1.28), while no difference was observed for the Pressure scale ($t(9) = 1.29$, $p = 0.27$, Cohen's d = 0.4). Furthermore, participants reported higher scores for Beat Saber in the UEQ in 4 out of 6 of the scales: Attractiveness ($t(9) = 3.7187$, $p = 0.0048$, Cohen's d = 1.176), Novelty (t(9) = 5.3780, $p = 0.0004$, Cohen's d = 1.7007), Stimulation ($t(9) = 4.5704$, $p = 0.0013$, Cohen's d = 1.4453) and Efficiency ($t(9) = 2.5697$, $p = 0.0302$, Cohen's d = 0.8126). Overall, participants reported a more positive experience in a related questionnaire both through the questionnaire scores and informal feedback when asked about their impressions.

Figure 2.8: Mean scores (± SEM) for the Enjoyment and Pressure subscales of the Intrinsic Motivation Inventory (IMI) following the Beat Saber (dark grey) and Control Classic (light grey) tasks.

These results highlight two important aspects of the Beat Saber paradigm. Firstly, data quality is comparable between Beat Saber and Control Key-Press. which demonstrates that an interactive, game-like environment can yield reliable measurements. Secondly, the greater enjoyment and immersion reported reveals the unique advantage this immersive and active method provides, which is improving participant motivation without compromising experimental validity.

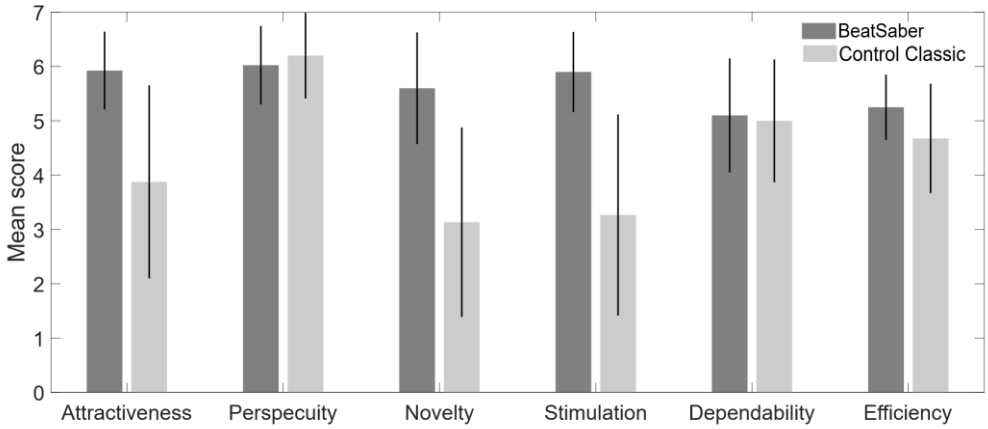


Figure 2.9: Mean scores (± SEM) for subscales of the User Experience Questionnaire (UEQ) following the Beat Saber (dark grey) and Control Classic (light grey) tasks.

General discussion

Mapping discrimination across color space is ultimately constrained by the cost of collecting large, high-quality datasets. Most existing data on color discrimination have been collected using psychophysical methods under highly controlled experimental conditions with static participants. While well tested, these methods can often be time consuming and uncomfortable, leading to sparse data and an under sampling of discrimination thresholds throughout color space. We aimed to explore how an immersive VR methodology could be used to measure color discrimination by embedding a standard odd-one-out 4AFC paradigm into a high-throughput and engaging VR game.

Using our method, we were able to replicate core findings from the color discrimination literature. We found that thresholds measured along the hue dimension of color space were generally smaller than those measured along chroma, aligning with previous work (Danilova & Mollon, 2014, 2016; Hedjar et al., 2025b; Krauskopf & Gegenfurtner, 1992; MacAdam, 1942). Further, this difference was not uniform across color space, with purple-ish colors having the lowest chroma-to-hue ratios while orange-ish had the highest (Danilova & Mollon, 2020; Hedjar et al., 2025a).

A key benefit of this ‘Beat Saber’ method is the rapid collection of quality data. With relatively little training participants were quickly able to respond at a rate of 1-1.5 trials per second. Each discrimination threshold we measured took approximately 3 minutes and 45 seconds. However, to assess data quality, our measurements were made with method-of-constant stimuli and a high number of repetitions and stimuli intensity levels (15 trials for each of 10 stimulus levels). Using adaptive staircase methods such as QUEST+ (Watson, 2017) it would be plausible to measure a single threshold in less than 50 trials, which would take approximately 1 minute and 15 seconds with our method. At this rate, full mapping of multiple planes becomes feasible within practical testing times.

Despite the rapid throughput and active nature of our task, we were able to accurately and reliably measure color discrimination thresholds. We compared this method with a control condition to assess the overall quality of the data, as the active nature of the task may introduce measurement errors due to task difficulty or motor control noise. Control Key-Press was matched to the ‘BeatSaber' method in every aspect except for the input method, using keyboard presses instead of swiping with the controllers. The measured thresholds were equivalent between our ‘BeatSaber’ method and Control Key-Press, except for chroma in the purple-ish

quadrant, where Beat Saber yielded slightly higher thresholds. Furthermore, goodness-of-fit analysis suggests that the data was well described by the psychometric model, with rejection rates being similar between 'BeatSaber' and the controls, and consistent with those typically reported in psychophysical research (Jäkel & Wichmann, 2006). These results suggest that, apart from minor differences, the psychophysical measurements collected with our 'BeatSaber' method are overall consistent and reliable, and the inherent difficulty of the task did not impact performance.

It is possible that the reliability of this method stems from high participant engagement and attention during the active task. While traditional psychophysical methods aim to achieve precise measurements via highly controlled experiments, they can suffer from errors due to participant discomfort and attentional lapses. We formally measured the differences in engagement and enjoyment between the 'BeatSaber' task and a more classic psychophysics setting with another control condition (Control Classic). In this condition, the stimulus was static and centerd on a uniform grey background. Responses to the Intrinsic Motivation Inventory (IMI) and User Experience Questionnaire (UEQ) suggest that participants found the 'BeatSaber' task significantly more enjoyable. In the IMI, 'Interest/Enjoyment' subscale responses were significantly higher for the 'BeatSaber' task than the control. Further, participants did not report significantly higher levels of pressure, suggesting that our method achieved a good balance between engagement and difficulty. Responses from UEQ further corroborate this, namely that participants found the method more attractive, more novel and more stimulating than the control. Immersive and gamified methods may therefore benefit psychophysical data collection via increased engagement with the task.

An immersive, gamified, VR methodology offers an opportunity to examine perceptual measurements under motor-engaged conditions. In everyday vision, perceptual judgments are typically embedded within ongoing action and interaction with the environment. Traditional psychophysical paradigms, by design, isolate specific perceptual mechanisms under highly controlled conditions. While this approach has yielded foundational insights, it remains important to assess whether established perceptual measurements generalize to more active contexts. In the present task, participants performed whole-arm movements to indicate their decisions within a dynamic, immersive environment. Despite this increased motor involvement, we replicated established asymmetries in color discrimination, including the super-importance of hue and its variation across color space. These findings suggest that the geometric structure of color discrimination is preserved under immersive, action-based conditions.

This result bears on longstanding discussions regarding the relationship between perception and action. Some accounts have proposed that perception and action are processed through functionally and physiologically distinct visual pathways, namely the ventral stream supporting object identification (vision for perception) and the dorsal stream guiding action (vision for action) (Goodale et al., 1994; Goodale & Milner, 1992; Milner & Goodale, 2008; Mishkin et al., 1983). However, accumulating evidence indicates considerable interaction and overlap between the two during complex, goal-directed tasks (Franz & Gegenfurtner, 2008; van Polanen & Davare, 2015). Our current results show that fundamental properties of color discrimination remain stable when perceptual decisions are executed through immersive, goal-directed action.

So far, we have demonstrated that the 'BeatSaber' method is a reliable tool to collect perceptual data with sufficient quality. It is intuitive, quick to learn, and importantly, more engaging, which benefits motivation and attention. The rhythmic nature of the game offers unexpected advantages: our auditory system is highly attuned to rhythmic sound patterns (Thaut et al., 2002) and studies have shown that auditory rhythmic cues can entrain motor responses (Large et al., 2002; Thaut et al., 1998). Notably, in the 'BeatSaber' method, the stimulus presentation timing (500ms) matches that of lab-based experiments (Hedjar et al., 2025a, 2025b); despite requiring full-arm movements rather than simple button presses, performance is not disadvantaged, possibly because participants easily synchronize their actions to the beat, allowing precise and temporally consistent responses. This could be, for example, a natural way to implement speeded forced decisions in experimental settings. Overall, this method can support faster data collection, and due to the entertaining nature of the task it allows longer sessions with a reduced risk of attentional lapses.

There are of course limitations with immersive and active experimental tasks. The 'BeatSaber' task requires basic motor coordination and some practice, and not all participants would be able to perform at an acceptable level. Whereas traditional psychophysics can be undermined by attention lapses, active tasks like Beat Saber are more susceptible to motor slips that can be interpreted as perceptual errors. Careful design and practice sessions are necessary and can help balance these trade-offs. Further, researchers must be aware of the limitations of VR headsets themselves. As with traditional monitor-based experiments, the display and optical properties of the set-up must be factored into experimental design. Current generation VR headsets do not match the quality of many high-end displays used for perceptual research. This, however, is likely to improve with continued development and optimization of VR displays.

Nonetheless, our results add to a growing body of work suggesting that VR headset displays can be used to conduct research on color perception (Díaz–Barrancas et al., 2023; Gil Rodríguez et al., 2022; Rodríguez et al., 2024).

This work is part of an emerging framework in perceptual research that aims to study sensory and decision-making processes through more active behavior. Continuous psychophysics (Bonnen et al., 2015, 2017; Huk et al., 2018; Knöll et al., 2018; Straub & Rothkopf, 2022) has been an influential approach to this. By moving past the rigid structure of independent trials and instead eliciting continuous behavioural adjustments to a dynamic stimulus, it allows to model perception as an ongoing process guiding action. Virtual Reality provides complementary advantages by enabling immersive, interactive environments while preserving rigorous control over stimulus presentation (de Gelder et al., 2018; Tachibana & Matsumiya, 2022; Wilson & Soranzo, 2015). Studying color perception with a 'BeatSaber' like game was first pioneered by Aizenman et al. (Aizenman et al., 2024) to measure color category boundaries. Our work builds on this foundation by demonstrating that such an approach can be extended to the quantitative measurement of color discrimination thresholds, while formally validating both data quality and participant engagement.

Conclusion

By enabling faster and more engaging data collection without compromising psychometric fidelity, immersive paradigms offer a practical route toward constructing more comprehensive empirical maps of perceptual color space. Approaches of this kind may help overcome the sparse sampling that has historically constrained the field, bringing large-scale metric characterization of color space within practical reach. As display technologies continue to improve, such methods may further bridge controlled laboratory psychophysics and more naturalistic perceptual behavior in the quantitative study of color vision.

IV. Discussion

In the words of Chaparro (Chaparro et al., 1993), "Color is what eye sees best". This work explored how color is seen in the context of visuo-motor behaviour.

It is clear that color information is crucial to guide motor behaviour, as showed by its effect on action (Brenner & Smeets, 2004; Schmidt, 2002; Toth & Assad, 2002).

Color is involved in the control of movements because, even though only a small portion of neuron in MT has selectivity for color (S. Zeki, 1983c), they've been shown to respond to photometrically isoluminant stimuli (Charles & Logothetis, 1989; Gegenfurtner et al., 1994). This is possible because the individual MT neurons have their own isoluminant point, which differs across cells. As a result, they still produce a detectable population response to a photometrically isoluminant stimuli (White et al., 2006).

Nonetheless, there are differences in the way in the way different attributes such as luminance, color and motion are processed, as extensively discussed in previous sections. One important difference lies in the neural response latencies associated with the magnocellular and parvocellular pathways (Barbur et al., 1998; Maunsell & Gibson, 1992; Schiller & Malpeli, 1978). These differences can be investigated through both behavioural experiments in humans and physiological recordings in primates.

We investigate this aspect of the visual system through our eye-movement experiment.

Here, participants were asked a simple question that nevertheless reveals fundamental mechanisms of visual processing: which color appears brighter? Although this question may resemble the type of judgment we might make in everyday life, the processes underlying the answer involve complex interactions within the visual system.

In our paradigm, the critical factor lies in the action – an eye movement – used to report the decision, and in the time required to execute it. By examining how perceptual judgments vary as a function of eye movements latency, it becomes possible to understand the temporal dynamics of visual processing. Previous work has established that signals carried by S-cones are processed with a measurable delay relative to luminance signals, both in behavioural measurements and in physiological recordings (White et al., 2009; White & Munoz, 2011).

What's informative in our results is that the answer to the question "which color is brighter?" depends on the speed of the eye movement used to report the decision. When eye movements occur at very short latencies, the visual system appears to rely primarily on luminance information. Under these conditions, two photometrically equiluminant targets are chosen with

approximately equal probability. However, when the eye movements latencies are longer the perceptual judgment begins to incorporate chromatic information, resulting in a systematic shift toward choices determined by the chromatic properties of the stimuli.

These results suggest that luminance signals become available earlier than chromatic signals in the decision process, and that the relative contribution of these signals depends on the time available for visual processing before the movement is executed.

While interpreting the results in terms of S-cone contributions, it is important to acknowledge that the "S-cone" defined targets used in the main and control experiments did not systematically isolate S-cone signals. Rather, these stimuli produced higher S-cone contrast than the yellowish stimuli, without fully eliminating contributions from other cone mechanisms. Nevertheless, the pattern observed in our data strongly suggests that the increased contribution of S-cone signals plays a key role in the effects reported here.

As discussed earlier, luminance measures are not always reliable predictors of heterochromatic brightness perception, partly because the contribution of S-cones tends to be underestimated. What is particularly informative in the present results is that the weighting of these visual signals appears to depend on the temporal constraints imposed by the action used to report the perceptual decision.

These findings highlight the importance of considering perception in the context of action. Vision is our primary sense, and it is not a passive process. High-acuity vision is restricted to the fovea, meaning that clear perception requires continuous eye movements to sample different parts of the visual field. Through these movements, the visual system actively selects and samples relevant information from the environment. The natural visual world is also highly dynamic, so it's not surprising how tuned our visual system is to sudden change in the visual field. Our eyes are immediately drawn to these visual events, a reflection of the importance of detecting change and action.

Our experiment is simplification of our everyday visual experience: we fixate somewhere that attracts our attention, targets suddenly appear, and we direct our eyes towards the one that is more salient.

The different experimental conditions recreated situations that elicit very fast, automatic and luminance-driven eye movements through the Gap paradigm, and a more conscious, color-driven eye movements through the Overlap and smooth pursuit paradigm.

If we think about the real world, it's easy to understand why our visual system prioritize luminance information earlier than chromatic one. Luminance signals are fast, they are critical for detecting motion, and overall support rapid orienting responses.

Chromatic signals are fundamental for object identification, material perception and scene identification, but when speed, rather than accuracy, is prioritized, luminance dominates.
For this reason, eye movements provide a valuable window into perceptual decision-making. The fastest saccades can be partially reflexive, reflecting early stages of sensory processing before conscious deliberation occurs. By analysing these rapid responses, it becomes possible to observe how visual information is progressively integrated over time, revealing aspects of perceptual processing that would remain hidden in slower, explicitly reported judgments.
After investigating low-level aspects of perception, with the color discrimination experiment we turn to the idea that more elaborate actions can also be closely linked to fundamental color perception processes.
Not only accurate color perception is compatible with complex motor behaviour, some evidence seemed to suggest that perception performances could be enhanced by a more active task (Bennett et al., 2013), although this was not the case.
This could be explained by several factors. For instance, the initial studies reporting perceptual enhancements associated with action were conducted in mice, and it is possible that similar effects do not generalize to humans.
Another possible explanation is that, even if the task enhances the ability to discriminate colors, this improvement may not translate directly into the measured results because of noise introduced by motor errors. While the task was designed to be intuitive and easy to learn, it is inherently more prone to variability than a simple key press response. Executing a motor action in a dynamic environment requires additional resources and introduces a trade-off between engagement and precision.
Participants performed the task for approximately 60 to 75 minutes. At the beginning of the session, the learning curve was relatively steep, and participants often needed a short period of adaptation to become comfortable with the task. However, despite this initial difficulty, most participants were able to perform the task reliably after only a few minutes of practice. It is therefore reasonable to hypothesize that with extended training the influence of performance-related noise would decrease, potentially revealing more clearly any perceptual benefits associated with the active nature of the task.
What we can confidently state is that features introduced by this paradigm, such as the motion of the stimuli, the change in retinal size, and the complex motor request did not have a negative impact on the results when compared to a static, traditional psychophysical experimental setting.

This result is encouraging, because it suggests that the study of perception can move beyond the constraints of classical psychophysical settings. Traditional paradigms offer clear advantages in terms of experimental control and precision, but they cannot address every question equally well. More immersive and action-based approaches may provide insights into how perception operates under conditions that more closely resemble natural behaviour.

Furthermore, the "Beat Saber" method allows for fast data collection for a sustained amount of time while keeping participants engaged in the task, which is a great advantage when a large amount of data is needed.

While being an improvement, it is still not realistic to sample a color space relying solely on this method, as the effort would still be significantly high and strenuous because of the amount of data needed.

An upgrade that could be easily implemented is the use of an adaptive staircase procedure, such as the Bayesian QUEST+ method (Watson, 2017) instead of a method of constant stimuli. This methodology demonstrably accelerates the estimation of PSE estimation (Paire et al., 2023). In this case, it would require even less trials to compute a color discrimination threshold.

Overall, the "Beat Saber" method has a lot of potential as a tool for psychophysical experiments. It is easily adaptable to a 4 or 2 Alternative Forced Choice paradigm and has been, for example, applied to study the stableness of color categories (Aizenman et al., 2024).

For color discrimination, a potential follow up of the current experiment could be to add an adaptation feature to the paradigm. Adaptation has a strong effect on discrimination.

This was shown at first for luminance defined stimuli (Craik, 1938), and later for chromatic ones (W. Brown, 1952; Krauskopf & Gegenfurtner, 1992; Pointer, 1974). The VR setting would allow for a full field, immersive environment where the surrounding background could modulate adaptation throughout the session.

Another example could be to measure the contrast sensitivity function by displaying the stimuli on the face of the moving cubes and ask participants to slash horizontally or vertically based on the orientation of the gratings. It could be interesting to explore how the CSF is computed in a more dynamic setting, because it may reveal different tuning properties compared to classical, static measurements.

Another major improvement to our current design would be to record eye and hands movements during the task. Having such data available would provide a richer description of the processes behind perception in action.

Typically, in goal-directed actions, the eyes move to the target before the hand (Johansson et al., 2001; Neggers & Bekkering, 2000), providing the visual information that guides the

upcoming movement. Hands and eye-movements data would provide insight into the decision-making process, such as when the target is first visually selected, when the motor response is initiated, how long the decision stage lasts before the action.

The data from the eye movements recording alone is a direct measure of visual attention, an information that is extremely relevant in an environment where participants must perform fast and controlled actions. Where did they look first? How long did they fixate? Eye tracking would reveal how information is sampled before a choice is made.

Finally, comparing eye and hand movements could help telling whether incorrect responses are caused by perceptual misjudgements or motor execution mistakes. Overall, the additional data such as reaction times, velocity profiles and movement trajectories could help to paint a richer picture of the processes underlying perception in action, and observe the possible changes over time, especially as the participant becomes more confident with the task.

In addition to these behavioural considerations, the technical characteristics of the experimental apparatus are also critical when studying color perception.

For our study, we used a Meta Quest 3 because it is comfortable to wear and easy to set up for color calibration. A minor drawback is, as discussed, the lack of an eye tracking feature, but this didn't affect the main purpose of the experiment, which ultimately was to test color discrimination.

A question could be raised about the accuracy of the display in displaying the colors. When systematically evaluated in terms of their calibration performance, the Meta Quest 3 seems to yield the worst results compared to other headsets (Duay et al., 2025). The color reproduction fidelity varies significantly across the lenses: it is optimal around the center, but the precision degrades in the periphery. Luckily though, our experiment is designed so that the stimuli are positioned in the center of the visual field, meaning that the color characterization is intact. This is confirmed by our results too, as they are comparable to similar experiments performed on high quality monitor (Hedjar et al., 2025b).

There is, though, an small limitation caused by the display, which is the constraint of an 8-bit display compared to a 10-bit one. An 8-bit display can produce order of magnitude less numbers of colors: around 16.7 million colors versus over 1 billion colors. This, of course, limit the precision of the PSE estimates. Therefore, for future work, it would be interesting to test color discrimination thresholds with a better display. This doesn't diminish our results because ultimately, our goal was to test an improved paradigm for perceptual data collection.

To summarize, this work focused on how color perception is shaped under action. It spans from investigating the temporal dynamics of the simplest action we can perform, moving our eyes,

to a more complex, high-level task that involves making quick perceptual decisions to perform a motor movement. It contributes to highlight the link between action and color perception, something that has been underestimated greatly in the past.

The results presented here show that perceptual judgments about color are not fixed properties of the stimulus but can depend on temporal constraints imposed by an action such as eye movements. In particular, the timing of eye movements and motor responses can reveal different stages of visual processing, highlighting how sensory signals are progressively integrated before guiding behaviour.

Combining immersive environments, eye movements and action-based paradigms opens new opportunities for studying vision under conditions that are closer to natural behaviour and can help better understand how the brain transform sensory information into decision and actions in real-world contexts.

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Datum Unterschrift

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