Neural Networks 165 (2023) 1–18

Contents lists available at ScienceDirect

Neural Networks

journal homepage: www.elsevier.com/locate/neunet

Review

Motion perception based on ON/OFF channels: A survey

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ARTICLE INFO

Article history:
Received 5 November 2022
Received in revised form 2 April 2023
Accepted 17 May 2023
Available online 25 May 2023

Keywords:
Motion perception
ON/OFF channels
Selectivity
Neural modelling
Bio-inspired sensor
Machine application

ABSTRACT

Motion perception is an essential ability for animals and artificially intelligent systems interacting effectively, safely with surrounding objects and environments. Biological visual systems, that have naturally evolved over hundreds-million years, are quite efficient and robust for motion perception, whereas artificial vision systems are far from such capability. This paper argues that the gap can be significantly reduced by formulation of ON/OFF channels in motion perception models encoding luminance increment (ON) and decrement (OFF) responses within receptive field, separately. Such signal-bifurcating structure has been found in neural systems of many animal species articulating early motion is split and processed in segregated pathways. However, the corresponding biological substrates, and the necessity for artificial vision systems have never been elucidated together, leaving concerns on uniqueness and advantages of ON/OFF channels upon building dynamic vision systems to address real world challenges. This paper highlights the importance of ON/OFF channels in motion perception through surveying current progress covering both neuroscience and computationally modelling works with applications. Compared to related literature, this paper for the first time provides insights into implementation of different selectivity to directional motion of looming, translating, and small-sized target movement based on ON/OFF channels in keeping with soundness and robustness of biological principles. Existing challenges and future trends of such bio-plausible computational structure for visual perception in connection with hotspots of machine learning, advanced vision sensors like event-driven camera finally are discussed.

Contents

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https://doi.org/10.1016/j.neunet.2023.05.031
0893-6080/

Nomenclature

AV	Angular velocity
BC	Bipolar cell
DS	Direction selectivity
DSN	Direction selective neuron
DSTMD	Directionally small target movement detector
DVS	Dynamic vision sensor
EMD	Elementary motion detector
ESTMD	Elementary small target movement detector
HR	Hassenstein Reichardt
LGMD	Lobula giant movement detector
LMC	Large monopolar cell
LPLC2	Lobula plate/lobula columnar type II
LPTC	Lobula plate tangential cell
MAV	Micro-aerial vehicle
ND	Null (Non-preferred) direction
OF	Optic flow
PD	Preferred direction
RF	Receptive field
RGC	Retinal ganglion cell
SAC	Starburst amacrine cell
STMD	Small target movement detector

1. Introduction

Motion vision or called dynamic vision, the process of detecting surrounding movements by eyes, is ubiquitous amongst a huge number of animal species, and critically important for them to interact effectively, safely with surrounding objects and environments. Differently to image processing, motion vision acts as a central role of correlating visual signals in both space and time within field of vision, or receptive field (RF), in order to estimate movement direction. Therefore, motion vision provides animals, humans and artificially intelligent machines with essential cues for navigation and course control. To build a dynamic vision system, one smart choice is learning from neuroscience, studies on how animals and humans process visual signals efficiently to acquire meaningful, diverse motion cues.

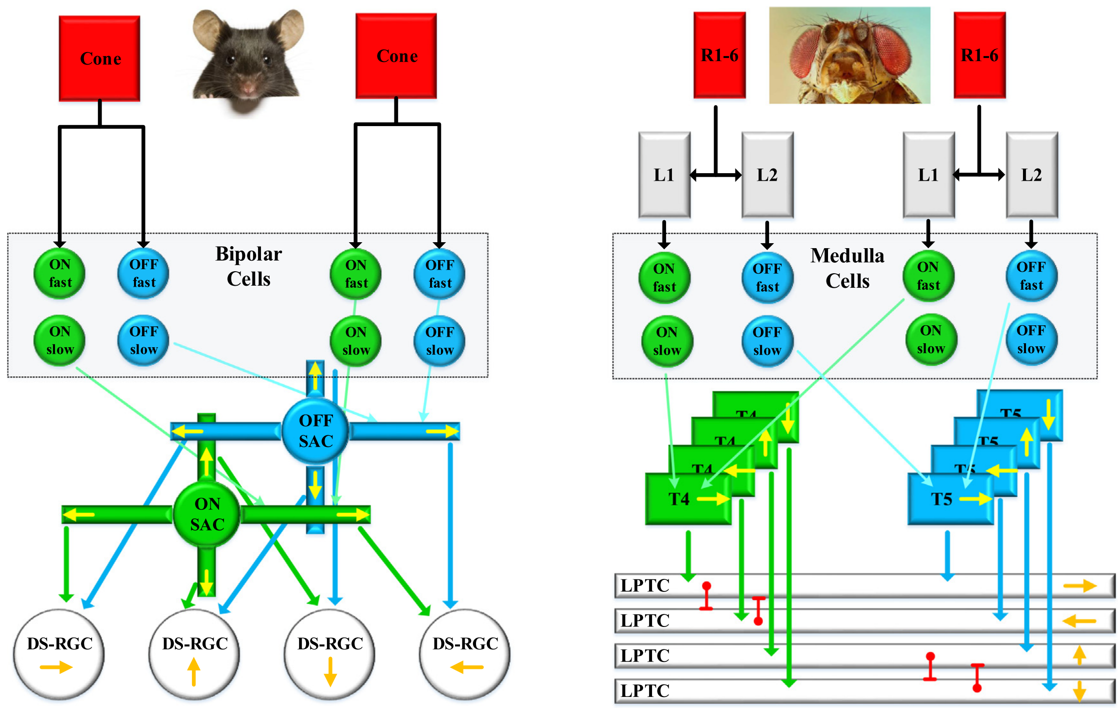
Movements inevitably induce brightness increments and decrements within RF. In the neural circuits underlying motion perception, neuro-scientists have found a novel structure, which separates early visual signals received at RF into ON/OFF channels (or called ON/OFF pathways) reliant upon brightness changes. Specifically, starting nerve cells of ON channels have a preference for dark-to-light luminance transitions (or **ON-contrast**) whilst those of OFF channels receive merely light-to-dark luminance transitions (or **OFF-contrast**). Such ON-contrast and OFF-contrast responses are processed within ON/OFF channels in parallel, delivered and communicated by different polarity interneurons resulting in specific direction selectivity (DS) to moving ON/OFF edges (Borst & Euler, 2011). Most importantly, this visual processing organisation has been found in the early vision systems of not only invertebrates like insects, but also vertebrates including mammals (Borst & Helmstaedter, 2015; Chariker, Shapley, Hawken, & Young, 2022; Clark et al., 2014) (see two typical paradigms in Fig. 1).

Neurons of this kind were discovered that can be dated back to the last century of 1910s (Cajal & Sanchez, 1915). The principles and neural mechanisms involved, however, have not yet been completely elucidated so far. Consequently, a few major concerns have arisen as follows: (1) **why** biological visual systems evolved to separate motion signals into parallel computation, at the cost though of more energy consumption; (2) **how** the received visual information bifurcates to be transmitted and communicated within ON/OFF channels in order to generate specific DS to diverse motion patterns including looming, translating and so forth; (3) **whether** this bio-plausible structure can be advantageous to build artificial vision systems to cope with real-world motion detection challenges.

Neuroscience research has partially responded to the former two concerns. However, to my best knowledge, none of studies have elucidated uniqueness and advantages of ON/OFF channels covering neural modelling and machine application. Currently, the vast majority of works are focusing on circuits, mechanisms, or postulated algorithms in animals' early vision systems for motion perception, elucidating the concepts of early visual motion splitting, processing, and transmission. On the other hand, the computational modelling works and corresponding applications based on ON/OFF channels have just emerged within the recent two decades. Through encoding polarity contrast change between moving target and background, some modelling works aim to mimic the early visual processing in parallel computation to achieve the functionality and selectivity of different movement detectors sensitive to diverse motion patterns including approaching and receding (movements in depth), translating, and small target motion, and so forth. Some modelling works aim at accomplishing visually guided flight behaviours like tunnel crossing, terrain following, landing, and etc. These works have, nevertheless, never been summarised and investigated together from the perspective of modelling ON/OFF channels for motion perception.

To fill this gap, this paper for the first time surveys relevant works via linking different disciplines including neuroscience, computer science, and robotics with emphasis laid on the advantages and uniqueness of ON/OFF channels in motion perception. This paper investigates the different functionality of ON/OFF channels in related neural models categorised into three types depending on their different DS. This also demonstrates the benefits of ON/OFF channels functionally implemented in machine vision. The main contributions of this paper are summarised as the following:

1. Currently known concepts of early visual motion processing based on ON/OFF channels are articulated.
2. Present computational modelling works and machine applications based on such bio-plausible signal-bifurcating structure to address real world problems are categorised and summarised.
3. This research highlights the significance of ON/OFF channels upon implementing different selectivity in motion perception.
4. The efficacy and robustness of ON/OFF channels in real-time visual processing like robotic systems against complex and dynamic environments are demonstrated.
5. This paper predicts future trends upon ON/OFF channels via bridging brain signal processing mechanisms to computer models and bio-inspired sensors.



(a) Mouse motion vision circuit (b) Fruit fly *Drosophila* motion vision circuit

Fig. 1. Schematic illustrations of two prominent examples of preliminary motion vision circuits in vertebrate and invertebrate. In the mouse's early vision systems, cone photoreceptors directly split the signal onto ON/OFF bipolar cells (BC). ON/OFF starburst amacrine cell (SAC) firstly show DS which pass both ON and OFF signals to local direction selective retinal ganglion cells (DS-RGC) sensitive to four cardinal directions. In the *Drosophila*'s early vision systems, photoreceptors R1-6 synapse onto large monopolar cells (LMC), L1 and L2, with a sign-inverting synapse. L1 and L2 are the entries to ON/OFF channels within the medulla. T4 and T5 are the first cells displaying DS to four cardinal directions. Wide-field lobula plate tangential cells (LPTC) in four stratified sub-layers integrate the DS signals from T4 and T5 cells with inhibitory connections between adjacent sub-layers. Notably, the input to T4 and T5 cells is provided by spatially displaced slow/fast medulla cells; the input to SAC by spatially displaced slow/fast BC has not yet been experimentally proved.

6. This paper exemplifies a bio-plausible research paradigm closing the gap between neuroscience and computational modelling with applications.

The taxonomy of this survey paper is given in Fig. 2. The rest of this paper is structured as follows: Section 2 introduces fundamental research and progress on motion vision systems. Section 3 gives mathematical description on signal bifurcation in motion perception. Sections 4–6 elaborate on three typical categories of motion sensitive neural models with emphasis laid on the advantages and uniqueness of ON/OFF channels. Section 7 presents relevant machine vision applications. Section 8 discusses challenges, future trends upon computational modelling of ON/OFF channels for motion perception, as well as hypotheses back to neuroscience. Section 9 concludes this survey. A ***Supplemental File*** complements Sections 4, 5 and 8 with figure representations.

每个部分的简述

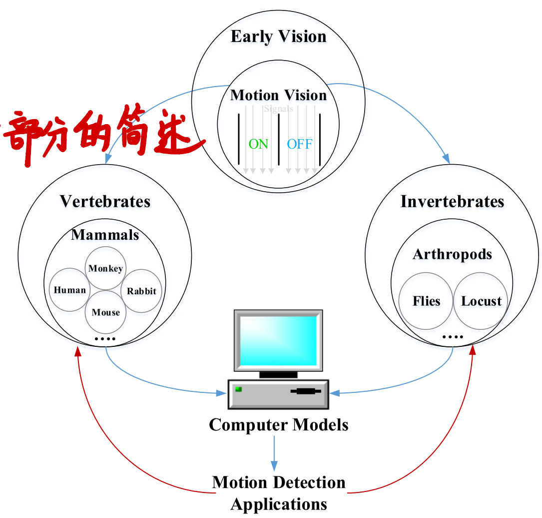


Fig. 2. Taxonomy of this survey: the blue pipeline indicates computational modelling with applications inspired by biological research into ON/OFF channels in motion vision systems of both vertebrates (mainly mammals) and invertebrates (mainly arthropods); the red pipeline indicates postulations back to biology through modelling and experimentation.

2. Fundamental research and progress

This section introduces representative early-stage biological and mathematical investigation on animals' preliminary vision systems for motion perception, as well as research progress.

2.1. Early-stage research

Neurons responding to visual motion in a direction-selective way are found in almost all sighted animal species. However, directional information is not explicitly encoded at the level of a single photoreceptor. Rather, it has to be computed from spatiotemporal signal correlation at least two photoreceptors. How this computation is implemented in terms of neural circuitry and membrane biophysics have remained the focus of intense research over many decades.

A century ago, Cajal and Sanchez looked into the early vision systems of flies and for the first time found the columnar T4 and T5 cells indicating mechanisms encoding visual signals in separate structures (Cajal & Sanchez, 1915). Starting at this

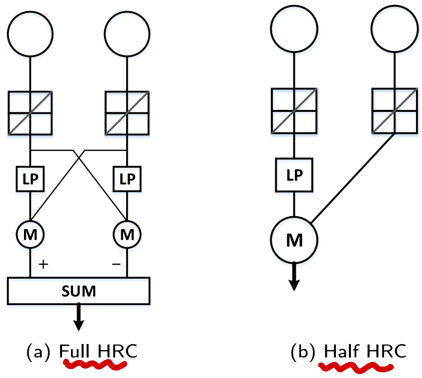


Fig. 3. Illustration of full (a) and half (b) HRC detector both with correlation between two spatially displaced cells: LP indicates the time lag represented by low-pass temporal filtering. M and SUM are short for multiplication and summation processes.

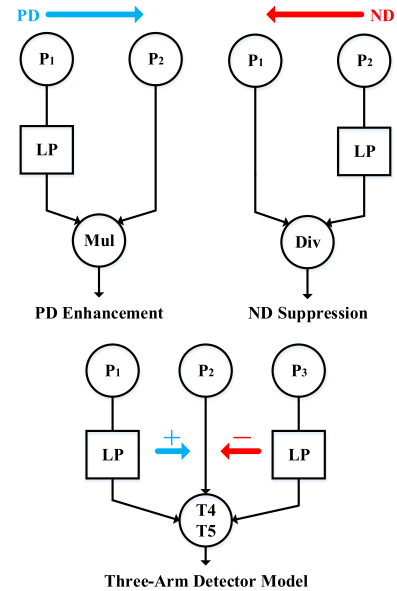


Fig. 4. Illustration of correlation-based motion detectors: the HRC model with preferred direction (PD) motion enhancement, the BL model with null direction (ND) motion suppression, and the latest finding of three-arm detector with both PD enhancement and ND suppression. P and LP denote photoreceptor and low-pass filtering of time latency. Mul and Div are short for multiplication and division.

work, in the 1950s, Gibson provided a first rigorous look at the perception of the visual world; the author pointed out that since the local motion vectors depend on the direction of the observer's movement, as well as on the structure of the environment, such a distribution of surrounding motion vectors can provide useful feedback signals (Gibson, 1950). Due to technical obstacles in anatomy, the internal structures and mechanisms of early visual processing were very hard to explore. The proposal of Hassenstein–Reichardt (HR) correlation model had became a milestone since 1956 (Hassenstein & Reichardt, 1956). This model postulates how visual signals are processed by brains to detect motion with directional information between spatially placed local detectors acting as a basis of understanding the brain's signal correlation mechanism till now (Borst & Egelhaaf, 1989; Borst, Haag, & Mauss, 2020; Egelhaaf, Borst, & Reichardt, 1989). The mathematical expression of a pairwise full-HR detector in Fig. 3 is given as the following:

$$R(t) = P_1(t-\epsilon) \cdot P_2(t) - P_1(t) \cdot P_2(t-\epsilon), \tag{1}$$

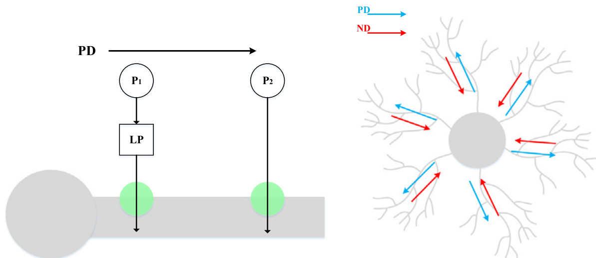
where R is the output of each pairwise motion detectors in space, with respect to time t. P_1 and P_2 are the inputs of two adjacent detectors, and ϵ is the delay (implemented by 'LP' in Fig. 3). Accounting for the generation of movement DS, this theory was found in keeping with the physiological recordings from internal neurons, and evidenced by a good number of follow-up studies on motion vision of fruit fly *Drosophila* including the exploration of ON/OFF channels (Borst & Euler, 2011; Borst & Haag, 2002; Borst et al., 2020; Borst & Helmstaedter, 2015).

There were also other remarkable works on biological motion perception visual systems. During the 1970s, the two LMC, L1 and L2, were discovered to respond to their six pre-synaptic photoreceptor inputs with a transient negative or positive signal at light-on (onset) or light-off (offset) response reminiscent of the putative mechanisms of ON/OFF channels (Järvilehto & Zettler, 1971). Strausfeld found most of the neurons in the third optic ganglion, the lobula, lie in a parallel structure which could provide possible pathways using different combinations of ON-type and OFF-type signals (Strausfeld, 1976). Also in the locust's visual brains, neuroscientists found the pre-synaptic interneurons of lobula giant movement detectors (LGMD) visual pathway respond selectively to onset and offset stimuli; this study postulates the existence of ON/OFF channels in locusts, for the first time at anatomical level (O'Shea & Rowell, 1976; O'Shea & Williams, 1974).

Later between the 1980s and 1990s, as the development of biological techniques, further steps were made to deepen the understanding of early visual processing circuits. More neuroscientists had given reasonable assumptions on the roles of ON and OFF parallel channels in arthropods (Laughlin, 1984), including dipterans (fruit fly, blowfly, dragonfly) (Coombe, Srinivasan, & Guy, 1989; Douglass & Strausfeld, 1998, 2001; Egelhaaf & Borst, 1992; Franceschini, Riehle, & Le Nestour, 1989; Jansonius & Hateren, 1991; Jansonius & van Hateren, 1993; Juusola, Uusitalo, & Weckstrom, 1995; O'Carroll, 1993; Ogmen & Gagne, 1990; Riehle & Franceschini, 1984; Strausfeld & Lee, 1991), and locusts (Osorio, 1987, 1991). Specifically, the fly visual systems stand out as the most prevalent models for exploring motion detection strategies (Borst & Egelhaaf, 1989; Egelhaaf & Borst, 1993; Egelhaaf et al., 1989).

On the aspect of vertebrates, the early-stage work commenced from the 1930s when Hartline illustrated the response of single optic nerve fibres to illumination on the retina with evidence supporting functional separation of luminance increments (ON) and decrements (OFF) in early visual motion processing (Hartline, 1938). After that, neuro-scientists researched into RF of cat and rabbit. During the 1960s, they found direction selective neurons (DSN) in the visual cortex that are sensitive to onset and offset stimuli (Barlow & Levick, 1965; Hubel & Wiesel, 1962; Oyster & Barlow, 1967). Consecutive works were taken to strengthen the comprehension on organisational and functional cells in cat's early vision system (Heggelund, 1981; Movshon, Thompson, & Tolhurst, 1978; Troyer, Krukowski, Priebe, & Miller, 1998). Notably, a research by Barlow and Levick demonstrated that the retina, unlike a simple pixel-array camera, already pre-processes visual information; the authors proposed a new correlation-based model accounting for the DS mechanism in rabbit's retina, named "Barlow-Levick" (BL) model (Barlow & Levick, 1965), as shown in Fig. 4. Specifically, this model suppresses non-preferred direction (ND) motion by a division operation between spatially displaced signals which has an opposite effect to the HR model with PD motion enhancement (see Fig. 4). To be precise, the mathematical expressions of PD enhancement and ND suppression are defined as follows, respectively:

$$R(t) = P_1(t-\epsilon) \cdot P_2(t), \;\; R(t) = P_1(t)/P_2(t-\epsilon). \tag{2}$$



(a) SAC motion detectors (b) SAC PD-ND motion

Fig. 5. Schematic illustration of direction selective responses in SAC dendrites: (a) PD motion detector along a single dendrite received signals from BC (two detectors shown) and wired to pathways with time lag at the proximal site, (b) direction selective responses in SAC dendrites with PD (centrifugal) and ND (centripetal) motion preference.

In 1980s, Schiller et al. summarised functions of ON/OFF channels in the visual systems of mammals including rabbit, monkey, and cat Schiller, Sandell, and Maunsell (1986); in this research, the authors pointed out the ON/OFF RGC are two major pathways originated at the BC for early visual motion processing; importantly, they also suggested the mammalian visual system has both polarity channels to yield equal sensitivity and rapid information transfer for both luminance increment and decrement facilitating high contrast sensitivity. In addition to that, Hildreth and Koch provided a comprehensive study and analysis on computational theory and neuronal mechanisms of visual motion (Hildreth & Koch, 1987); they summarised the models and algorithms in early motion detection and measurement, and moreover pointed out ON-centre and OFF-centre cells generate DS for ON and OFF edges in visual cortex of rabbit. Based on those, Clifford and Ibbotson gave insights into the models, cells and functions in both vertebrate's visual cortex and insect's optic lobes whereby the ON–OFF-type cells are sensitive to brightness increment and decrement in motion pre-filtering stage (Clifford & Ibbotson, 2002). As the retina is of great importance in animals' early vision systems, a few studies reviewed fundamentals of retina as the elementary building block of vision including BC that receive signals bifurcated into ON/OFF channels (Euler, Haverkamp, Schubert, & Baden, 2014; Masland, 2001). A study also outlined theoretical and mathematical expressions on DS to discriminate between PD and ND motion stimuli whereby DS-RGC respond to both ON and OFF polarity motion (Escobar, Pezo, & Orio, 2013).

2.2. Recent progress

Driven by the development of new biological techniques like genetic tools, the recent two decades have witnessed much progress on vertebrates' visual systems towards understanding the circuits, cells and mechanisms underlying motion perception (Borst & Euler, 2011; Borst & Helmstaedter, 2015; Chariker, Shapley, Hawken, & Young, 2021; Chariker et al., 2022; Clifford & Ibbotson, 2002; Euler et al., 2014; Masland, 2001). In vertebrates, the retina is crucial for early visual motion processing, that is structured by five cell types constituting inner and outer plexiform layers: photoreceptors, horizontal cells (HC), BC, SAC, and RGC (see Fig. 1(a)). Most importantly, the ON–OFF dichotomy in vertebrate's retina was evidenced by Westheimer in 2007 (Westheimer, 2007). The roles of ON-subtype BC implementing the low-pass filtering were investigated later by Ichinose, Fyk-Kolodziej, and Cohn (2014). In vertebrates' retina, the BC are the first nerve place separating motion information into ON/OFF channels, also showing temporal properties for signal correlation accordingly (Euler et al., 2014; Strettoi, Novelli, Mazzoni, Barone, & Damiani, 2010).

In the light of DS, RGC are the primary sites displaying the core motion attribute, as revealed by research into rabbit (Fried, Munch, & Werblin, 2002), cat (Troyer et al., 1998), mouse (Sun, Deng, Levick, & He, 2006), and primates (Berzhanskaya, Grossberg, & Mingolla, 2007; Chariker, Shapley, & Young, 2016). More precisely, there are three groups of RGC, i.e., the ON–OFF-RGC, the ON-RGC, and the OFF-RGC, amongst which the ON–OFF-RGC were first explored to be directionally selective (Borst & Euler, 2011; Borst & Helmstaedter, 2015) whereby action potential responses are substantially stronger when the stimulus moves in the cell's PD than moving oppositely in the cell's ND. Accordingly, a central concern herein arises that how the DS in RGC is formed. Neuroscientists have found SAC between BC and RGC in the inner plexiform layer of retina shape the DS (Borst & Euler, 2011; Borst & Helmstaedter, 2015; Kim et al., 2014). As illustrated in Figs. 1(a) and 5, the SAC themselves exhibit direction selective responses exposed to moving stimuli: its output is increased against centrifugal (soma-to-tip) PD stimuli whilst decreased against centripetal (tip-to-soma) ND stimuli. A study using three-dimensional reconstruction and simulation of retina elaborated that the DS is generated, asymmetrically, along the dendrite of SAC with PD motion enhancement; the time lag is put forth with the BC before synapse on the proximate side of dendrite and there is no delay for the distal one (Kim et al., 2014). Accordingly, the response of SAC is amplified only when the motion signals from different BC arrive at the dendrite, simultaneously (Fig. 5).

Regarding invertebrates, there has also been significant progress on crabs (Carbone, Yabo, & Oliva, 2018), insects including various dipterans (blowfly (Nordström, 2012), hoverfly (Nordström, Barnett, & O'Carroll, 2006; Nordström & O'Carroll, 2006), dragonfly (Dunbier, Wiederman, Shoemaker, & O'Carroll, 2012), fruit fly *Drosophila* (Arenz, Drews, Richter, Ammer, & Borst, 2017; Borst, 2018; Drews et al., 2020; Fisher et al., 2015; Joesch, Schnell, Raghu, Reiff, & Borst, 2010; Strother et al., 2017), locusts (Jones & Gabbiani, 2010; Peron, Jones, & Gabbiani, 2009; Simmons, Sztarker, & Rind, 2013; Wernitznig et al., 2015)). Here the progress on ON/OFF channels in motion perception will be highlighted upon fruit fly *Drosophila* and locust as prevailing system paradigms.

Fly is a most famous model system to study biological motion detection strategies (Borst, 2014; Borst & Euler, 2011; Borst et al., 2020; Borst, Haag, & Reiff, 2010; Borst & Helmstaedter, 2015; Franceschini, 2014; Serres & Ruffier, 2017). Fig. 6 draws the signal tuning map in ON/OFF channels. Specifically, motion perception starts at retina layer with columnar arranged photoreceptors (R1–R8), amongst which the outer R1–R6 convey signals to LMC of lamina layer (Rister et al., 2007; Vogt & Desplan, 2007). The LMC encode motion by luminance changes whereby onset and offset responses are separated into ON/OFF pathways: L1 with its downstream medulla-intrinsic (Mi)-1 and trans-medulla (Tm)-3 interneurons of medulla layer relay light-on response to T4 neurons; L2, L3 with their downstream Tm-1, Tm-2, Tm-4, and Tm-9 interneurons relay light-off response to T5 neurons (Fisher et al., 2015; Rister et al., 2007; Strother, Nern, & Reiser, 2014). Direction selective motion signals of ON/OFF-contrasts to four cardinal directions are generated by T4 and T5 cells in a feed-forward manner, respectively (Arenz et al., 2017; Borst et al., 2020; Fisher et al., 2015; Maisak et al., 2013). As the terminal of ON/OFF channels, LPTC in four stratified sub-layers of the lobula plate pool the DS signals from T4 and T5 neurons where the same direction selective response is gathered into an identical sub-layer (Borst et al., 2020). At the same time, lobula plate-intrinsic (LPi) interneurons convey inhibition to adjacent sub-layers with

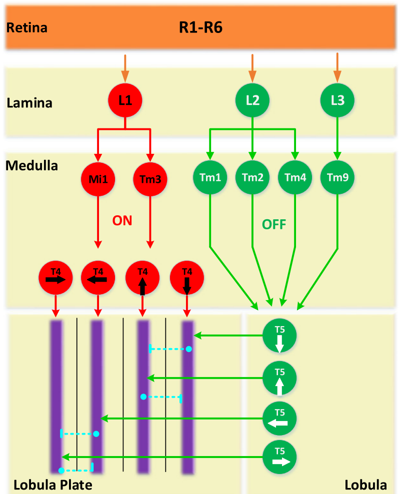


Fig. 6. Schematic diagram of *Drosophila*'s ON/OFF pathways for motion perception. Retina R1–R6 neurons convey motion information to lamina LMC which split signals into parallel ON/OFF channels denoted by two coloured neurons and pathways; the direction selective signals are carried by T4 and T5 cells to four sub-layers in stratified lobula plate, where T4 and T5 cells with the same PD signals converge on the same sub-layer of LPTC; the DO response is delivered by LPi interneurons between neighbouring LPTC sub-layers (dashed lines). Image courtesy of Fu and Yue (2020b).

reverse DS through sign-inverting interactions, thus, forming the direction opponent (DO) response (Badwan, Creamer, Zavatone-Veth, & Clark, 2019; Mauss et al., 2015). Eventually, horizontal and vertical sensitive systems collect signals from the LPTC toward sensorimotor control (Joesch et al., 2010). Regarding the generation of DS, Haag et al. proposed a different view of three-arm detector with both PD enhancement and ND suppression accounting for responses of T4 and T5 cells (Haag, Arenz, Serbe, Gabbiani, & Borst, 2016) (Fig. 4). Recently, there are also studies on visual projection neurons at deeper brain with elaborated placement to cover the whole region of LPTC. One assembly called lobula plate/lobula columnar type II (LPLC2) neurons demonstrate ultra-selectivity to radial motion of objects expanding particularly from the centre view (Klapoetke et al., 2017).

Locusts have evolved to possess very robust looming perception systems to escape from collision dangers (Wernitznig et al., 2015). A group of wide-field motion sensitive neurons, i.e., the LGMD located in the lobula layer of locust's visual brain play crucial roles in looming perception pathways for sensorimotor control (O'Shea & Rowell, 1976; O'Shea & Williams, 1974; Rind & Simmons, 1992; Rind et al., 2016; Simmons & Rind, 1992; Simmons et al., 2013). LGMD's pre-synaptic neurons respond selectively to light-on and light-off stimuli that could be accomplished in the medulla of locust's visual systems (Osorio, 1987, 1991). More recently, a research group found that (1) the LGMD represents slightly stronger response to OFF-contrast than ON-contrast stimuli (Jones & Gabbiani, 2010), and (2) the possible overlap of the ON/OFF pathways in LGMD's pre-synaptic dendrite implies the ON/OFF channels play roles in locust's dynamic vision (Peron et al., 2009). After that, Wernitznig et al. proposed the synaptic connections between first-stage visual neurons, photoreceptor and two lamina cells, in the locust's looming sensitive pathways (Wernitznig et al., 2015). Like the LMC in *Drosophila*, the L1 and L2 neurons in locusts are postulated to play roles for detecting ON/OFF polarity motion with fast spatiotemporal changes in light levels, as the possible entries of ON and OFF pathways. However, further investigation is required to make sure the L1 and L2 are contributing to the directionally selective motion detection pathways like in flies. Recalling the initial two major concerns on (1) how visual signals bifurcating to parallel ON/OFF channels, and (2) why animals processing motion in parallel visual computation at probably more energy cost, the possible reasons have been given from the perspective of neuroscience within this section.

2.3. Commonalities

After elaborating on the progressive studies on motion vision systems, the commonalities between motion vision systems of vertebrates and invertebrates herein are concisely summarised which could deepen the understanding of motion perception strategies based on ON/OFF channels. A century ago, Cajal noted striking similarities between the neural circuits underlying vision in vertebrates and flies (Cajal & Sanchez, 1915), which were supported by structural and functional studies over the past few decades. Surprisingly, genetic studies have also revealed that vertebrates and invertebrates may share a common evolutionary origin. Hence, Sanes and Zipursky reviewed shared features of first several layers in vertebrates and flies (Sanes & Zipursky, 2010). Clark et al. proposed that flies and humans, though with disparate visual brains and different scales of neuronal networks, share a similar motion encoding–decoding strategy in natural scenes (Clark et al., 2014); to deal with complex natural environments, fly and human visual systems estimate the combined direction and ON–OFF polarity contrast of moving edges using triple correlations of motion detectors in space and time. Several commonalities between different animal species herein can be abstracted as follows:

1. Evolved over hundreds-millions years, the most prominent commonality is the splitting of motion into ON/OFF channels at the retina of vertebrates, and the optic lobe of invertebrates. Precisely, such signal bifurcation happens right at photoreceptor-to-bipolar synapse in vertebrate's **retina**, whilst at LMC in invertebrate's **optic lobe**.
2. ON/OFF channels are a governing principle for DS in motion perception. The computation of DS is done separately in ON/OFF pathways. Such computation ends at the very next synapse until the DS is produced: in optic lobe, T4 (ON) and T5 (OFF) cells jointly synapse onto LPTC; the same is observed in vertebrate's retina where SAC from ON/OFF channels contact ON–OFF type RGC.
3. Another similarity is the representation of DS along four orthogonal directions. This general strategy seems to be a robust solution for how to compute the direction of visual motion within neural circuitry.

3. Signal bifurcation

This section gives rigorous computational description of signal bifurcation with attention upon the starting nerve cells, i.e., the BC in vertebrates, and the LMC in invertebrates both splitting visual motion signals into parallel computation. Mathematically, the membrane potential of ON/OFF-type units at position (x, y), time t is described by a state variable $U(x, y, t)$ whose dynamics is defined by the following differential equation:

在位置在 x,y, 时间为t处的输入亮度，Eex，Ein 为固定值，分别为1和-1.

$$\begin{aligned}\frac{dU(x,y,t)}{dt} &= I(x,y,t)\cdot(E_{ex}-U(x,y)) \\ &+ I(x,y,t-1)\cdot(E_{in}-U(x,y)) \\ &+ g_{leak}\cdot(V_{rest}-U(x,y)),\end{aligned} \tag{3}$$

where $I(t)$ and $I(t-1)$ are the input luminance at two discrete time steps, and $I \in [0, 1]$. V_{rest} denotes the resting potential (or leakage reversal potential) which the nerve cell will adopt if

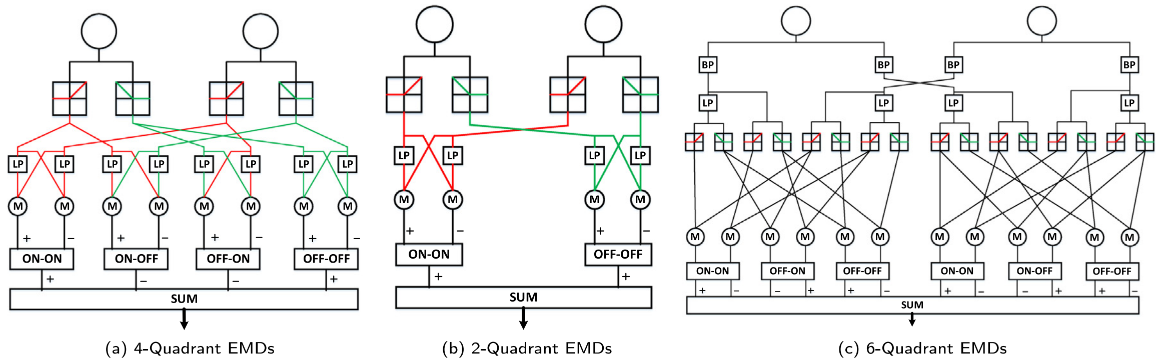


Fig. 7. Different combination forms of ON/OFF EMD: BP, LP denote band-pass, low-pass filtering; M, SUM indicate multiplication, summation, respectively. Fig. 3 and this figure together illustrate the evolution of EMD from single-channel to dual-channel processing.

no stimulus received, and $V_{rest} \in [E_{in}, E_{ex}]$. $E_{ex} = 1$ and $E_{in} = -1$ are the excitatory and inhibitory synaptic values, respectively, which confine a nerve cell's dynamic range as $U(x, y) \in [E_{in}, E_{ex}]$. If no responsive bias is set between ON-type and OFF-type neurons, i.e., both equally responding to the contrast polarities (ON-contrast and OFF-contrast), $V_{rest} = 0$. g_{leak} is the leakage conductance that indicates the total passive ion flow through the cell membrane. Accordingly, the activity of starting nerve ON/OFF-type cells separating different polarity signals is given by

$$\tilde{U}(x, y, t) = \gamma \left([U(x, y, t) - \Theta]^{+} + [-U(x, y, t) - \Theta]^{+} \right), \tag{4}$$

where γ is a gain factor and Θ is a local threshold (or called "clip point") normally set at a tiny positive real number. $[\alpha]^{+} \equiv \max(0, \alpha)$.

In the follow-up sections, three main categories of motion perception models based on the formulation of ON/OFF channels will be surveyed with investigations on the advantages and uniqueness of such signal bifurcation mechanism in forming different selectivity to directional motion and small-sized target movement. The vast majority of presented methods in this paper are based on biological research into insects' dynamic vision systems, perfect paradigms to construct artificial vision systems in order to solve real-world motion detection challenges, effectively and efficiently.

4. ON/OFF EMD models

Within this section, elementary motion detectors (EMD) based on ON/OFF channels are introduced. The variations of ON/OFF EMD models fitting with different motion detection objectives and course controls are also presented. The advantages of ON/OFF channels in EMD are investigated as the final part of this section.

4.1. EMD models based on ON/OFF channels

In the last century, Gibson developed a framework of optic flow (OF) to perception and action in which OF can be defined as a vector field of the apparent motion of objects, surfaces, and edges in a visual scene (Dauxere, Serres, & Montagne, 2021; Gibson, 1950; Serres & Ruffier, 2017). This framework is extremely useful for different course controls including terrain following, tunnel centring, speed adjustment, landing tasks and so on. Bio-robotic researchers and engineers have made practical use of the OF-based strategy to facilitate the stabilisation of flying machines (Expert & Ruffier, 2015; Franceschini, 2014). To compute the OF to generate local directional information, the EMD is an excellent toolkit that is also a seminal and classical computational structure for studying biological motion perception (Franceschini, 2014; Frye, 2015; Fu, Wang, Hu, & Yue, 2019; Hassenstein & Reichardt, 1956).

Prior to the initial findings of ON/OFF channels, motion signals are transmitted and correlated in a single pathway regardless of polarity contrasts using 'full-wave rectifier' (Fig. 3). In early-stage modelling research, a visual model represented responsive preference to only step sequences of brightness increase (ON–ON) or decrease (OFF–OFF) according to the H1 neuron response of fly visual system (Anstis & Rogers, 1974). Two neural models were proposed to simulate ON–OFF units in flies (Ogmen & Gagne, 1990; Sarikaya, Wang, & Ogmen, 1998). Notably, Franceschini et al. pioneered the splitting of EMD inputs into ON-EMD and OFF-EMD operations encoding separately light and dark edges for micro-simulation of receptors in RF (Franceschini, Riehle et al., 1989; Franceschini, Riehle, & Nestour, 1986). Moreover, the evidence for 'half-wave rectification' in the high-pass arms of EMD to achieve the functionality of starting nervous cells of ON/OFF channels has been given in Franceschini, Pichon, and Blanes (1989), Reiff, Plett, Mank, Griesbeck, and Borst (2010).

In the recent decade, there have been several bio-plausible theories representing different combination forms of ON-EMD and OFF-EMD (Joesch, Weber, Eichner, & Borst, 2013) (Fig. 7). Interestingly, these models all coincide in the latest biological findings that DS signals are generated at T4 and T5 neurons prior to the stratified LPTC (Badwan et al., 2019; Maisak et al., 2013). Accordingly, the medulla and lobula layers are the suitable places implementing these ON/OFF EMD representing signal bifurcation and non-linear computation.

Specifically, after the splitting of motion, ON/OFF-type signals interact in either the same or the opposite polarity pathways. In this regard, some studies argued for different detector combinations (Gabbiani & Jones, 2011). Firstly, a 4-quadrant (4-Q) detectors model represents communications between both the same and the opposing polarity signals, i.e., ON–ON, ON–OFF, OFF–ON, and OFF–OFF (Eichner, Joesch, Schnell, Reiff, & Borst, 2011); this model is mathematically equivalent to the HR model with symmetric pair of connections in Fig. 3(a). Another 2-Q detectors model was proposed by Eichner et al. through electrophysiological recordings from LPTC in *Drosophila*, which depicts signal interactions within only the same-sign channels, i.e., ON–ON and OFF–OFF, parallelly (Eichner et al., 2011; Joesch et al., 2013). The authors also pointed out a small fraction of original signals can pass through into the motion-detecting circuits revealing that not only the transient luminance change but also the permanent brightness can be encoded for motion perception. Besides, a more complex 6-Q detectors model debated that either the ON/OFF channel conveys motion information with both ON-contrast and OFF-contrast through behavioural response observed in *Drosophila* (Clark, Bursztyn, Horowitz, Schnitzer, & Clandinin, 2011). This model also highlights the extraction of ON/OFF edges prior to the correlation of motion signals, implemented by spatial band-pass filtering.

These different alternatives of ON/OFF EMD have significantly deepened our understanding of how the OF can be computed to correlate local ON/OFF-contrast features in parallel, although there is little evidence on signal communication between ON/OFF channels. However, such ON/OFF motion detectors have been tested by merely synthetic visual stimuli in simple scenarios. To construct ON/OFF EMD for addressing more complex, real-world motion detection challenges, some computational models have been proposed. The first category of models mimic the functionality of LPTC in flies. Wang et al. proposed an LPTC neural model for estimating the shifting direction of cluttered background OF (Wang, Peng, & Yue, 2017). The main novelty of this paper is simulating the functionality of Tm-9 neurons in OFF pathway for wide-field motion detection. As the LPTC are sensitive to translating motion along four cardinal directions, a few works provided insights into the revealed internal neural circuits in *Drosophila* in order to generate DS through multiple neuropile layers in parallel ON and OFF pathways. Specifically, a visual neural network with ensembles of 2-Q ON/OFF EMD was proposed to extract translating ON/OFF moving edges in front of visually cluttered backgrounds with improved speed response in contrast to previous methods (Fu & Yue, 2017b). Further to it, the authors demonstrated efficacy of spatiotemporal motion pre-filtering mechanisms prior to ON/OFF channels for decoding the direction of merely foreground translating object against cluttered background OF (Fu & Yue, 2020b).

Another well-established type of velocity-tuned EMD model was proposed by Franceschini et al. which is also called the "time-to-travel" method (Franceschini, Pichon, & Blanes, 1992; Moeckel & Liu, 2007; Serres, 2018). In contrast with the classic EMD, this scheme represents the output of the velocity-tuned EMD dependent of the ratio between the photoreceptor angles in space, as well as the time delay for each pairwise contrast detection photoreceptors.

As a variation of EMD, a few motion perception models inspired by honeybee's visual systems have been put forward to estimate angular velocity (AV) using only visual cues (Cope, Sabo, Gurney, Vasilaki, & Marshall, 2016), rather, an amazing ability to guide a variety of flight behaviours including centring behaviour in tunnel crossing, terrain following, landing, and so forth (Ibbotson, Hung, Meffin, Boeddeker, & Srinivasan, 2017). Inspired by ethological research on honeybees, a few modelling works based on ON/OFF EMD were proposed to model the honeybee's AV detection visual systems, gradually simulating AV-guided flight behaviours. Wang et al. put forward a neural model with each single AV detecting unit correlated by three input detectors within ON/OFF channels with an averaging process at the final stage to indicate AV-tuned response (Wang, Peng, Baxter et al., 2018). After that, the authors proposed a neural network model named "angular velocity decoding model" (AVDM) to match the biological findings that honeybees usually maintain constantly at an AV around 300 °/*s* in flight, and conducted corresponding behavioural simulations including tunnel crossing, terrain following (Wang et al., 2021; Wang, Fu, Wang, Peng, Baxter et al., 2019; Wang, Fu, Wang, Peng, & Yue, 2019). This model utilises 2-Q ON/OFF EMD as the foundation, and incorporates a texture decoding pathway for the purpose of estimating AV with higher precision using only visual information. Compared to the state-of-the-art AV-estimation methods regardless of encoding ON/OFF polarity signals, the AVDM demonstrates larger independence on spatial frequency, and invariance to image contrast and noise. This series of research consolidates the effectiveness of ON/OFF channels in estimation of AV, which can be applied as powerful sensory systems for aerial robots working at GPS denied environments.

主要在说 AVDM 模型.

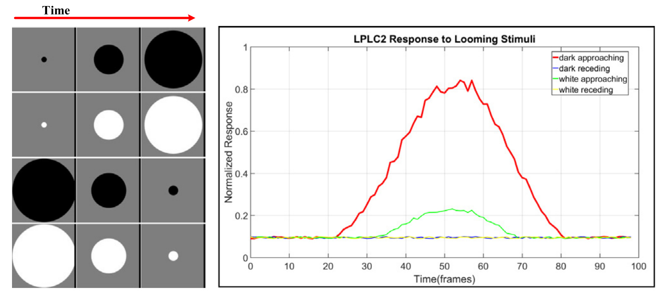


Fig. 8. LPLC2 model based on ON/OFF channels responds to dark/white radial motion. The ON-contrast and OFF-contrast features are encoded separately. ON/OFF channels play important roles to shape the LPLC2 with ultra-selectivity to only dark radial motion. The model reacts to white radial motion as well but with much weaker output. Neither of dark and white targets receding from the eye excites the LPLC2.

As another extension of ON/OFF EMD, LPLC2 neurons in flies cover entirely the four stratified layers of LPTC, correlate response on four cardinal directions so as to shape the ultra-selectivity to only looming objects from centre of RF. Recent computational works aimed at sculpting the elaborate characteristics of such neuronal ensemble (Hua, Fu, Peng, Yue, & Luan, 2022; Zhou, Li, Kim, Lafferty, & Clark, 2022). The ON/OFF channels in Hua et al. (2022) act effectively to separate diverging motion cues of ON and OFF edges to form responsive preference to darker looming target over other stimuli, which reconcile with the corresponding physiological findings (Klapoetke et al., 2017). Fig. 8 compares the response of LPLC2 model to looming and receding.

4.2. Advantages of ON/OFF channels in EMD

Doubling visual motion processing pathway, at first sight, appears as a profligate strategy of nervous system. From the perspective of computational modelling and hardware implementation, Franceschini gave deep thoughts of advantages upon splitting motion into ON/OFF-EMD (Franceschini, 2014; Franceschini, Riehle et al., 1989). Specifically, movement induces luminance increment and decrement, and the detection of motion requires temporal correlation between spatially displaced, multiple detectors. When a dim object crosses RF, its leading and trailing edges give rise to light-off and light-on responses, respectively. The motion sensing neurons should be excited by both the places regardless of the sign of luminance change. Accordingly, processing motion in separate polarity channels with both positive information can fit well the spatiotemporal correlation of detectors for either PD enhancement or ND suppression. In this regard, Borst also pointed out that the splitting of motion and handling of only positive signals could alleviate the biophysical problem of correlating two input signals with brightness decrements and increments (Borst, 2018).

Here we look deeper into the advantages of ON/OFF channels in EMD models from the perspective of modelling. ***Supplemental File*** illustrates the results of comparative investigation. Firstly, the *Drosophila* motion perception model in Fu and Yue (2020b) works effectively to extract foreground translating OF from cluttered moving background by decoding the direction of moving target into response of horizontally and vertically sensitive systems, i.e., positive and negative response to PD and ND movements, respectively. To demonstrate the benefits of ON/OFF channels in this model, the internal processing structure is modified to correlate signals with single-channel HR structure in Fig. 3(a). **Fig. S1** compares the responses whereby the model with ON/OFF channels perceive the foreground translating OF against cluttered moving background very robustly. In contrast, the single-channel model is greatly affected by movement of cluttered background motion, cannot decode the direction of foreground OF, accurately. Therefore, the ON/OFF channels work effectively to separate the correlation of moving ON–ON, OFF–OFF edges in order to defend directional motion cues against background dynamics.

Secondly, the AVDM in Wang et al. (2021) can estimate the AV using only visual cues that meets well the ground truth data from behavioural experiments of honeybees. The efficacy of ON/OFF channels for AV-tuned behaviours like tunnel crossing has been validated in Wang et al. (2021), Wang, Fu, Wang, Peng, bibetal (2019). Here such structure is also replaced by the single-channel HR model (Fig. 3(a)) in a virtual bee flying through a tunnel, stimulated bilaterally by sine-grating-patterned walls. In tunnel crossing, the real bees show centring behaviour by balancing bilateral AV received at RF. **Fig. S2** compares the simulation outcomes of tunnel crossing. Obviously, the simulated bee with visual processing of ON/OFF channels represents excellent centring behaviour to cross the patterned tunnel converging at the centre line after starting from different initial places, in line with the real bee's behaviour. On the other hand, the virtual bee loses such robust capability of stabilising bilateral AV.

5. ON/OFF LGMD models

Within this section, lobula giant movement detector (LGMD) models based on ON/OFF channels are surveyed. This section also investigates the uniqueness of ON/OFF channels to achieve different looming selectivity between LGMDs to ON-contrast and OFF-contrast.

5.1. LGMD models based on ON/OFF channels

There are many LGMD models for collision perception in various scenarios, as reviewed in Fu, Hu, Liu, and Yue (2018), Fu, Wang et al. (2019). The vast majority of LGMD models nevertheless do not involve the parallel visual computation on encoding ON-contrast and OFF-contrast, separately. There are two main causes: (1) the physiological evidence in support of ON/OFF channels in locust's looming perception neural pathways is very limited compared to flies; (2) the solution of single-channel processing is acceptable of handling looming perception tasks against a variety of scenarios including vehicles (Yue, Rind, Keil, Cuadri, & Stafford, 2006), robots (Yue & Rind, 2006), and UAVs (Salt, Howard, Indiveri, & Sandamirskaya, 2019). What is the motivation of introducing the computational structure and mechanism of ON/OFF channels in LGMD modelling? 动机？

In general, the ON/OFF channels in LGMD models are driven by (1) realising different selectivity to looming darker or brighter object relative to background, (2) improving robustness of model against dynamic, complex environments. Before elaborating on these two points, the physiology of LGMD neurons will be briefly introduced.

In the locust's visual pathways, a group of LGMD neurons has been found in which the LGMD-1 and LGMD-2 have been functionally and anatomically identified in the lobula area so far. These two neurons are physically neighbouring to each other (see **Fig. S3**). Both LGMD neurons respond to rapid expanding image of an approaching object representing an imminent collision or a strike from predator (Rind & Bramwell, 1996; Rind et al., 2016; Simmons & Rind, 1997; Simmons et al., 2013). The physiological response of LGMD-1, however, differs from the LGMD-2's in a number of ways. First, LGMD-2 is not sensitive to ON-contrast, i.e., a brighter or white looming object whereas LGMD1 is. Sztarker and Rind investigated the development of LGMD in locusts from adolescent to adult (Sztarker & Rind, 2014). They clarified that compared to LGMD-1, LGMD-2 matures earlier in

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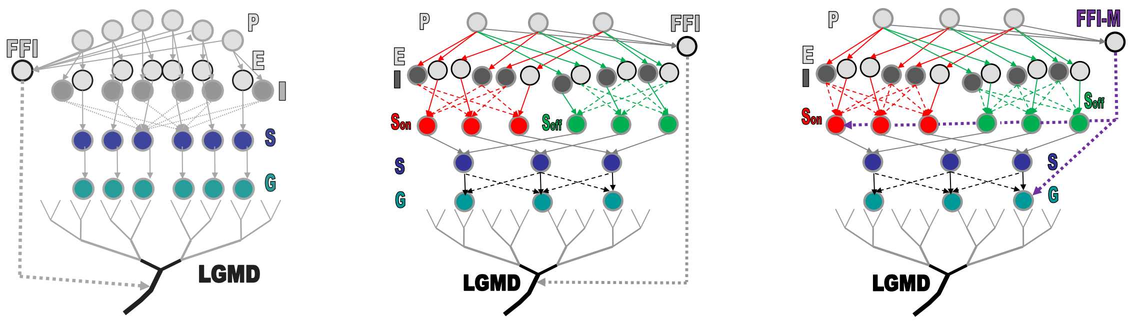
juvenile locusts living mainly on the ground playing a critical role of signalling approaching predators from the sky. Accordingly, LGMD-2 has been revealed to respond merely to OFF-contrast. Second, LGMD-2 does not respond to darker objects that recede at all, while LGMD-1 is often excited though very briefly (Fu, Hu, Peng, Rind, & Yue, 2020). As locust grows up, the visual environments become more complex due to flying behaviours. LGMD-1 gradually complements LGMD-2 for looming perception, and can deal with flight-related colliding scenarios.

To cope with real world scenes with comparatively higher complexity than closed, and simply-structured experimental environments, Keil et al. proposed two seminal works on LGMD-1 based on ON/OFF mechanisms in 2003 (Keil & Rodriguez-Vazquez, 2003) and 2004 (Keil, Roca-Moreno, & Rodriguez-Vazquez, 2004). Their proposed methods showed good performance in adverse situations including low-contrast objects, highly textured background; the two models also represented non-linear properties of mapping input signals to membrane potential reminiscent of biological LGMD-1. Based on non-linear theory, Badia et al. proposed a visual neural network to match well the bio-plausible invariance of looming perception against stimuli with varied shapes, textures, and approaching angles (Badia, Bernardet, & Verschure, 2010). In this research, the authors proposed that ON/OFF channels encode luminance increment (onset) and decrement (offset) responses respectively. In addition, the transmission of inhibitory signal is delayed relative to the excitation in ON channels; conversely, the excitatory signal is delayed relative to the inhibition in OFF channels. Recently, Olson et al. investigated the feed-forward, global, and lateral inhibition in a numerical model of LGMD-1 for predicting responses to looming stimuli where OFF-type cells were modelled (Olson, Wiens, & Gray, 2021).

To separate the different selectivity between LGMD-1 and LGMD-2, Fu et al. proposed a series of computational modelling works based on parallel ON/OFF channels to implement the presynaptic neural networks of both LGMD-1 and LGMD-2. Specifically, the authors proposed different spatiotemporal competitions between excitations and inhibitions in ON/OFF channels to implement the functionality of biological LGMD-1 (Fu, Hu, Peng, & Yue, 2018), as shown in Fig. 9(b) which was the first work to introduce parallel ON/OFF channels into the classic, multi-layered LGMD neural network model in Fig. 9(a). For the purpose of improving the performance in highly variable environments, Fu et al. modelled adaptive inhibition mechanisms mediated by feed-forward inhibition (FFI) in ON/OFF channels (see Fig. 9(c)). This model outperforms previous methods to detect merely imminent crash rather than other kinds of movements in cluttered moving backgrounds, and complicated vehicle driving scenarios (Fu et al., 2019; Fu, Wang, Peng, & Yue, 2020). Before introducing ON/OFF channels in LGMD, there was no modelling works realising the specific selectivity of LGMD-2 to only OFF-contrast stimuli. In this regard, such signal bifurcation structure is of great usefulness. Fu and Yue proposed a seminal modelling work on LGMD-2 by splitting preliminary motion into ON and OFF channels with different delayed signal processing and non-linearity (Fu & Yue, 2015). This model demonstrated similar selectivity like biological LGMD-2 to darker objects approaching rather than any other kinds of movements. Based on that, the authors implemented the LGMD-2 model into a micro-mobile robot for signalling potential 应用 collision dangers in visual navigation (Fu, Yue, & Hu, 2016). As the neural circuitry of LGMD-2 does not involve the FFI pathway like the LGMD-1's, Fu et al. proposed a more rigorous visual neural network to implement the LGMD-2 and its pre-synaptic circuits (Fu, Hu et al., 2020), as exhibited in Fig. 10. In this research, the authors proposed the concept of "biased-ON and OFF channels" to implement the specific selectivity of LGMD-2



(a) Single-channel LGMD-1 model (b) ON/OFF LGMD-1 model (c) ON/OFF LGMD-1 model

Fig. 9. Schematic illustrations of different LGMD neural network models: P, I, E, S, G, FFI indicate photoreceptor, inhibition, excitation, summation, grouping layers and feed-forward inhibition, respectively. **This illustrates the evolution of LGMD from single-channel to dual-channel processing**: (a) Yue and Rind (2006), (b) Fu, Hu, Peng et al. (2018), (c) Fu, Wang et al. (2020).

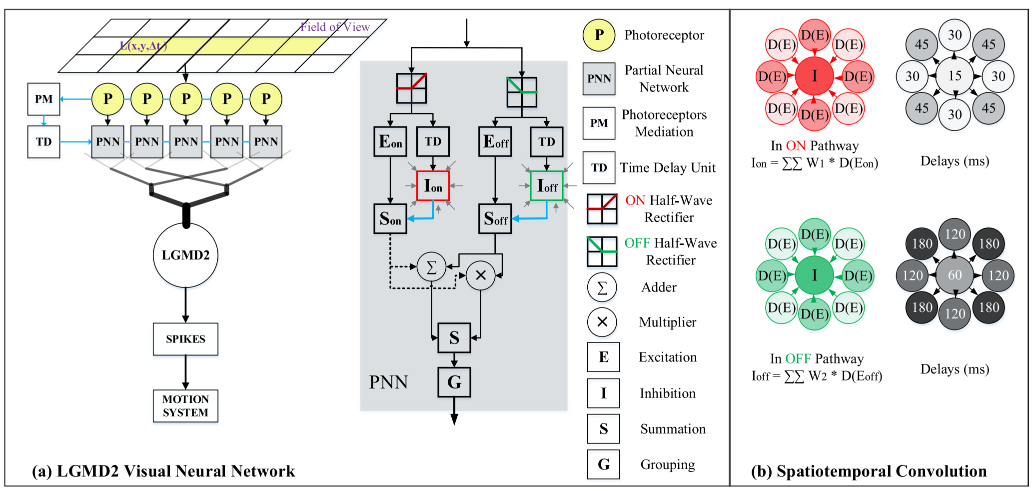


Fig. 10. Schematic illustration of the seminal LGMD-2 neural network model with ON/OFF channels to implement specific selectivity to looming stimuli elicited by darker objects. **This elucidates the uniqueness of ON/OFF channels in separating the different selectivity between LGMD models**. Image courtesy of Fu, Hu et al. (2020).

whereby the ON channels are suppressed by stronger inhibitory signals in contrast to OFF channels. This model fulfils all the basic responsive selectivity of LGMD-2 revealed by early biological studies.

To further investigate the different collision selectivity between LGMD models, some hybrid LGMD models were developed. Two LGMD neural networks integrated the functionality of LGMD-1 and LGMD-2 based on ON/OFF channels for implementation in micro-mobile robot guiding reactive collision avoidance in dynamic environment containing multiple moving robot agents (Fu, Hu, Liu, & Yue, 2017), as well as artificially critical traffic scenarios (Fu, Sun, Liu, Hu, & Yue, 2021). These studies all verified the computational simplicity and effectiveness of ON/OFF LGMD-1 and LGMD-2 models addressing real world challenges as embedded vision systems to guide timely collision detection-and-avoidance. Considering the homology between ON/OFF motion vision of flies and locusts, Fu et al. further sharpened up the collision selectivity through coordination and competition between LGMD-1, LGMD-2, and two horizontally sensitive LPTC ensembles with embodiment in micro-robot vision for real time collision detection (Fu & Yue, 2020a). In comparison with single neuron computation, this hybrid model shows extreme selectivity to proximity feature by frontal approaching stimuli.

5.2. Advantages of ON/OFF channels in LGMD

Shaping the looming selectivity to merely approaching objects, and separating the selectivity to ON/OFF-contrast are always challenging the artificial vision systems, especially in complex and dynamic environments. Many algorithms and mechanisms have been proposed to enhance the DS in LGMD models (Fu, Wang et al., 2019). Differently to the previous research, this paper focuses on articulating the efficacy and uniqueness of ON/OFF channels in tuning diverse looming selectivity to fulfil the characteristics of different LGMD circuits.

Compared to the ON/OFF EMD models, the generation of DS, i.e., the loom-selective response of ON/OFF LGMD models is totally different. The core computation in LGMD is the spatiotemporal interaction between local ON/OFF excitations and inhibitions, mathematically described as

$$
\begin{aligned}
E(x,y,t) &= \iint P(u,v,t)G_{\sigma_1}(x-u,y-v)\,du\,dv,\\
I(x,y,t) &= \iiint E(u,v,\tau)\Psi(t-\tau)G_{\sigma_2}(x-u,y-v)\,du\,dv\,d\tau,\\
S(x,y,t) &= [E(x,y,t)-\alpha\cdot I(x,y,t)]^{+},
\end{aligned}
\tag{5}
$$

where P indicates the signal after split at either ON/OFF channel, and E, I, S are short for excitation, inhibition, and summation in either ON/OFF channels (refer to Fig. 10). G_{σ_1} and G_{σ_2} are spatial convolution matrix obeying Gaussian distribution. $\Psi(t)$ denotes a temporal function whereby the ON/OFF inhibition signal is delayed, relative to excitation. Accordingly, the signal after such competition is delivered further to the LGMD.

By tuning the spatial and temporal mechanisms in ON/OFF channels, the different DS of LGMD models can be achieved. Specifically, in the LGMD-2 (Fu, Hu et al., 2020) (Fig. 10), the bias is put forth in ON channels whereby the inhibition is stronger. We herein also show the effect of bias in OFF channels vice versa. **Fig. S4** compares the different loom-selectivity to dark/white objects moving in depth. Accordingly, from the modelling perspective, ON/OFF channels can implement three types of loom-selective neurons to (1) both ON-contrast and OFF-contrast, i.e., the LGMD-1; (2) only OFF-contrast, i.e., the LGMD-2; (3) only ON-contrast, unidentified in locust's visual brain.

6. ON/OFF STMD models

This section introduces small target movement detectors (STMD), and highlights the irreplaceable role of ON/OFF channels in such category of motion sensitive neural models. Moving targets at long-sight distance usually appear as small-sized dim speckles that are always blurred into background and difficult to separate from noise. Accordingly, small moving targets cannot provide sufficient visual features, such as colour, shape, and texture for motion perception. These set obstacles for traditional computer vision methods to extract small target motion cues from especially cluttered and dynamic background.

In this regard, biological motion perception neural systems are competitive for extracting such small target features, at a distance and early. Inspired by insects physiology, there are mainly two categories of STMD models, i.e., the elementary-STMD (ESTMD) and the directionally-STMD (DSTMD). Notably, both categories are based on the signal bifurcation into ON/OFF channels for motion filtering and correlation to achieve size and direction selectivity to small targets. From the biological perspectives, the most significant difference between STMD and other motion sensitive neurons like DSN and LGMD is the exquisite size selectivity (Nordström, 2012; Nordström et al., 2006; Nordström & O'Carroll, 2006). More precisely, the STMD represents peak responses to targets subtending $1\sim3^\circ$ of RF, nevertheless has no response to larger bars (typically $> 10^\circ$), or to wide-field grating stimuli. A darker moving small target induces luminance decrement followed quickly by increment at a local site of RF; whilst a brighter moving small target induces luminance increment followed quickly by decrement. In another word, a small moving target unavoidably induces continuous, quick luminance changes at a local position with the combinations of ON–OFF, or OFF–ON. Such transient change can be effectively encoded by ON/OFF channels in early stages of visual processing.

Accounting for such characteristics, Wiederman et al. proposed a seminal model for perceiving small target, i.e., the ESTMD, which implements the specific size selectivity of STMD neurons in insects (Wiederman, Shoemaker, & O'Carroll, 2008) (see Fig. 11b). This model comprises non-linear filtering based on the fly optics, the first-order large monopolar cells, and the rectifying transient cells whereby signal bifurcation is implemented in the medulla layer. The main achievement of this numerical model is for the first time matching neural properties described for STMD, such as contrast sensitivity, height tuning and velocity tuning. Another important finding through experiments is the ESTMD model can discriminate small target and its background without the need for relative motion cues. To achieve such specific functionality, the authors demonstrated a recombination of ON/OFF channels at a single unit in the lobula layer, to form an output corresponding to the ESTMD response, as the following equation:

$$R(x,y,t) = a \cdot ON(x,y,t) + b \cdot D\,[OFF(x,y,t)] \\ + c \cdot ON(x,y,t) \cdot D\,[OFF(x,y,t)]\,. \tag{6}$$

$\{a, b, c\}$ is a combination of coefficients. Notably, the signal in OFF channel is delayed relative to the signal in ON channel in order to realise the specific selectivity to darker target motion of OFF-contrast. Such supra-linear computation was later supported by a physiological study (Wiederman, Shoemaker, & O'Carroll, 2013). Furthermore, this can also provide the selectivity to white target motion of ON-contrast by correlating a delayed signal in ON channel with a non-delayed signal in OFF channel as follows:

$$R(x,y,t) = a \cdot D\,[ON(x,y,t)] + b \cdot OFF(x,y,t) \\ + c \cdot D\,[ON(x,y,t)] \cdot OFF(x,y,t). \tag{7}$$

After that, the ESTMD has been developed to perform more robustly in high dynamic range natural scenes, and the model output is highly correlated to the velocity of stimulus rather than other background statistics, such as local brightness or contrast (Wiederman, Brinkworth, & O'Carroll, 2010). The ESTMD has also been transformed in discrete temporal domain with a physiologically accurate log-normal filter to approximate the small target detecting characteristics in continuous time domain, more applicable to hardware implementation (Halupka, Wiederman, Cazzolato, & O'Carroll, 2011). Based on it, the authors further incorporated a winner-take-all network of local feature detectors in order to direct the gaze of a camera mimicking the behavioural 'saccades' in fixating the background (Halupka, Wiederman, Cazzolato, & O'Carroll, 2013). Besides, Wang et al. improved the performance of ESTMD model in dynamic visual clutter by implementing a new lateral inhibition mechanism (Wang, Peng, & Yue, 2016).

In terms of biology, some STMD neurons have also demonstrated DS (Nordström et al., 2006; Nordström & O'Carroll, 2006). Specifically, these neurons respond strongly to small target motion oriented along PD, but show weaker or even fully opposing response to ND motion. The generation of DS requires correlation between spatially displaced motion detectors similarly to EMD. Obviously, ESTMD on its own structure of correlating temporal

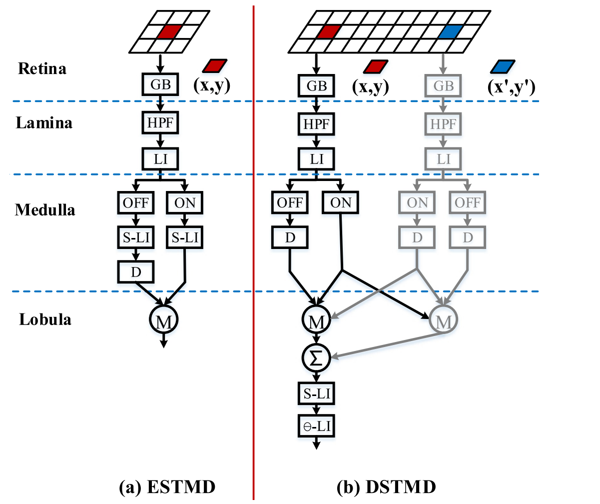


Fig. 11. Schematics of (a) ESTMD and (b) DSTMD computational structure: GB, HPF, LI, S-LI, Θ-LI, D, M are abbreviated respectively for Gaussian blur, high-pass filter, lateral inhibition, second-order lateral inhibition, lateral inhibition on direction Θ, time delay, multiplication. **This shows the evolution of STMD models with the decoding of DS**. Image courtesy of Fu, Wang et al. (2019).

change of a single unit in ON/OFF channels cannot fulfil DS in motion perception. To address it, different methods have been proposed to correlate small target motion. Firstly, a few ESTMD models in connection with EMD, i.e., the ESTMD-EMD and the EMD-ESTMD, were put forward to implement DS (Wiederman & O'Carroll, 2013a, 2013b). More concretely, the ESTMD-EMD indicates that the ESTMD cascades with the EMD, while the EMD-ESTMD indicates that the EMD cascades with the ESTMD.

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Another method of DSTMD was recently proposed by Wang, Peng and Yue (2020) (see Fig. 11a). **Fig. S5** illustrates how the specific DS is achieved by the DSTMD via correlating spatially displaced, temporally delayed ON/OFF motion detectors. Mathematically, such ON/OFF signals correlation can be described as

$$R(x_1, y_1, t; \theta) = ON(x_1, y_1, t) \cdot \{\Gamma\big(OFF(x_1, y_1, t)\big) + \Gamma\big(ON(x_2, y_2, t)\big)\} \cdot \Gamma\big(OFF(x_2, y_2, t)\big), \tag{8}$$

where $x_2 = x_1 + \alpha\cos\theta$, $y_2 = y_1 + \alpha\sin\theta$, θ indicates a specified direction amongst eight of DSTMD. $\Gamma(x)$ denotes a temporal Gamma function acting as delay. Building upon DSTMD and ESTMD, Wang et al. further proposed a contrast pathway in Wang, Peng, Zheng and Yue (2020), and a feedback mechanism in Wang, Peng, and Yue (2018) to improve the model performance by reducing false positives in detection of small target motion against cluttered dynamic backgrounds. Compared to the ESTMD, the DSTMD models nevertheless require very high input sampling frequency to maintain robust performance of decoding the direction of small target motion. The high computational complexity of DSTMD calculating motion in eight directions at every system-update could heavily restrict the scalability to real time applications.

可扩展性

Compared to the modelling of EMD and LGMD, the signal bifurcation is unique, and indispensable for constructing STMD models, since all the current STMD visual systems are based on such a bio-plausible structure which is prerequisite for the perception of small target motion.

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7. Machine vision applications

This section introduces machine vision applications based on neural modelling of ON/OFF channels. Regarding robotic vision, some visual models have been applied effectively in ground mobile robot navigation. Firstly, collision detection and avoidance are two crucial steps for any mobile machine running effectively and interacting safely within dynamic environments. A prerequisite for conducting an appropriate and timely escape is the reliable collision prediction. The first ON/OFF LGMD-2 model (Fu & Yue, 2015) was successfully implemented in embedded vision of a mobile-micro robot under extremely constrained computing resources for detecting only darker objects approaching. The authors also carried out systematic robot experiments including arena tests with which the robot navigated freely in an arena and escaped from imminent collision guided by the ON/OFF LGMD models (Fu et al., 2017; Fu, Hu et al., 2020; Fu, Wang et al., 2020; Fu et al., 2016). To investigate the viability of ON/OFF LGMD models in more dynamic robot scenarios, Fu et al. physically simulated critical traffic to corroborate the robustness of LGMD-1 and LGMD-2 visual systems functioning together as embedded vision module for timely collision prediction (Fu et al., 2021). Notably, the ON/OFF channels functioned smoothly in robot's visual module for real time collision-detecting tasks.

Motion tracking is another influential, bio-mimetic embodiment of ethological behaviour in autonomous robots. Hence, some bio-plausible motion perception models have been successfully applied to address real world visual tracking challenges. A series of works was proposed by Bagheri et al. for realising a physiological response of "facilitation" , i.e., enhancement of neuronal response to a stimulus following stimulation (Bagheri, Wiederman, Cazzolato, Grainger, & O'Carroll, 2014, 2015a, 2015b, 2017). Specifically, the facilitation stage boosts responses to small targets moving along continuous trajectories against textured backgrounds. The model was effectively applied as a building block in an autonomous robot to mimic insect's motion tracking in different natural scenes (Bagheri, Cazzolato, Grainger, O'Carroll, & Wiederman, 2017). In respect of a behavioural research (Bahl, Ammer, Schilling, & Borst, 2013), the *Drosophila* motion vision model was implemented on board a micro-mobile robot for motion tracking with a closed-loop response to fixation (Fu, Bellotto, Hu, & Yue, 2018; Fu & Yue, 2017a). Most importantly, these works demonstrated the insect vision based on ON/OFF channels can be parsimonious and effective solutions to robots.

On the aspect of vehicle vision, the ON/OFF EMD model proposed early by Franceschini can be implemented in their developed ground vehicle (Pichon, Blanes, & Franceschini, 1989), and various types of flying vehicles including MAV (Franceschini, 2014; Pudas et al., 2007; Ruffier, Viollet, Amic, & Franceschini, 2003; Viollet & Franceschini, 1999). Autonomous driving is another technology-leading domain that embraces different sensing modalities and methodologies. Optical approaches are superior in providing rich description on surrounding movements, and perform freely of road infrastructure. By introducing ON/OFF channels in ground vehicle vision, Fu et al. investigated the effectiveness and robustness of ON/OFF LGMD models in many real physical, off-line scenarios where crashes happen (Fu et al., 2019; Fu, Hu et al., 2020; Fu, Hu, Peng et al., 2018; Fu, Wang et al., 2020). Specifically, the models of ON/OFF channels work effectively to encode separately the motion cues, decrease the intra-variance of image dynamic features corresponding to rapid expanding dark or light contour, enhance the robustness against background noise. For example, the ON/OFF LGMD-2 model can extract very effectively the potential crash by darker approaching targets in daylight vehicle navigation (Fu, Hu et al., 2020). In the future, these visual system modules of ON/OFF channels necessitate on-line testing for practical use and volume production of bio-inspired sensors in vehicle industry.

8. Challenges, future trends, hypothesis

The main focus of this paper falls upon the ON/OFF motion vision. Through previous sections, we have shown the advantages and uniqueness of ON/OFF channels in formulating diverse motion sensitive neural models specialising in different motion perception tasks. Bio-inspired intelligence recently has been considered as a promising alternative to classic methods in AI. The benefit of bio-inspired intelligence stems from its resource efficiency (or parsimony) especially in terms of mass and power towards hardware implementation. As the development of neuroscience, researchers should not simply apply existing AI algorithms but exploit insights from natural intelligence to promote AI technology. Within this section, I will discuss on existing challenges of motion perception models, and predict future trends in connection with cutting-edge bio-inspired sensors and hotspots of machine learning. At last, I will summarise hypotheses of computational modelling and implementation back to neuroscience.

8.1. Challenges

The introduced neural models in this paper belong to model-based approaches. There are also data-driven machine learning approaches for motion detection and classification. Each category of methods has advantages and disadvantages, and there is no agreement on what is the best method, since it depends exactly on the application. <1>

For model-based methods, the existing challenges mainly stem from different trade-off such as (1) latency vs. power consumption and accuracy, (2) sensitivity vs. bandwidth and processing capacity. It is also difficult to quantify such trade-off in order to optimise the model performance, and to improve adaptability (or robustness). For example, the bio-inspired visual systems are advantageous in their low-power, data-free, real-time implementation, and efficiency. However, the accuracy of motion perception especially in complex and dynamic environments emerges as big problem for bio-inspired modelling methods. One possible reason is the EMD (Fu & Yue, 2017b, 2020b, 2021), LGMD (Fu, Hu et al., 2020; Fu, Hu, Peng et al., 2018), STMD (Wang, Peng & Yue, 2020; Wang, Peng, Zheng & Yue, 2020; Wiederman et al., 2008) models process signals in merely feed-forward structure lacking feedback communications. In addition, the system parameters are always manually configured depending on biological research and optimisation of performance for specified visual tasks. Because there is currently no comprehensive dataset to train such bio-plausible motion perception models, <2> the learning methods are rarely involved in EMD, LGMD, STMD modelling works. Despite that, a data-driven method, i.e., the evolutionary computation has been utilised to improve the robustness of LGMD model against very complex real world scenarios by evolving in visual environments of a small-sized vehicle-crash dataset (Fu, Wang et al., 2020).

These motion perception models are also operated merely on frame-based camera systems, but biological vision handles signals in continuous time domain. Moreover, a confinement for current motion perception models is the biological substrates of ON/OFF channels remain largely unknown due to technical obstacle in neuroanatomy and neurophysiology.

Another big challenge is incorporating motion perception models in formulating long-term, efficient end-to-end systems from perception to control and actuation. For example, active vision that couples perception and control becomes a hotspot in computer vision and robotics. The stage of motion perception is prerequisite to visuomotor response. In this regard, the bio-plausible computation can be very efficient, low-latency solution. Besides, utilising prior knowledge from neuroscience (e.g. local mechanism or network functionality) can undoubtedly leverage high performance and low energy consumption.

8.2. Future trends

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Potential for bio-inspired sensors. To bridge biological visual systems to artificial vision systems and intelligent machines, the final pattern of computational model is certainly reflected on vision sensors. I am quite optimistic that such bio-plausible computation methods can be implemented as neuromorphic visual models in hardware. This would be extremely advantageous to achieve higher processing speed, larger scale, real-time solutions.

To be more specific, the neuromorphic visual sensors are realised in two different shapes. One is utility of high-performance circuits such as the field-programmable gate array (FPGA), which captures images with high resolution and high frame rate in order to significantly enhance the visual model's spatial sensitivity and temporal response for designs with critical requirements. For instance, the ON/OFF EMD model has successful FPGA implementation (Aubépart, El Farji, & Franceschini, 2004; Aubepart & Franceschini, 2007).

Another type is single-chip solutions featuring compact size and specialised functions which is usually implemented by complementary metal–oxide–semiconductor (CMOS), and very large-scale integration (VLSI) processes (Moeckel & Liu, 2010; Stephane Viollet, Menouni, Kerhuel, & Franceschini, 2010). For example, the insect's photoreceptors in compound eyes have been emulated by silicon retina (Vanhoutte, Mafrica, Ruffier, Bootsma, & Serres, 2017). An European consortium developed a miniature vision sensor named "curved artificial compound eye" (CurvACE) to mimic the fruit fly *Drosophila*'s compound eye (Floreano et al., 2013). Although it is much larger than the fly's eye, it consists of 630 ommatidia and 630 photoreceptors which resembles many properties of the *Drosophila*'s eye. Importantly, the authors stated that any pair of EMD based time-of-flight scheme with split ON/OFF channels is able to estimate the AV of a natural panorama ranging up to 360° within a wide span of illuminance (Franceschini, 2014).

This kind of integrated chip can also be utilised as an optical sensor for further applications. In the recent decade, the event-based camera, also called dynamic vision sensor (DVS) emerges as very powerful, bio-inspired sensor that remarkably differ from conventional frame-based cameras. The DVS features low latency, high speed, and high dynamic range, as summarised in Gallego et al. (2020). Biological principles and computational primitives drive the design of event camera hardware and some of the event processing algorithms such as spiking neural networks. Most importantly, such vision sensor can report ON and OFF events asynchronously and independently for every single pixel depending on brightness increase (ON) or decrease (OFF), a milestone much closer to biological visual processing observed by neuroscientists. Hence, to build small, efficient and reactive computational systems, the ON/OFF channels appear as a source of inspiration for event-based processing which ideally match the core features of DVS.

Regarding motion perception using DVS, a number of methods deal with optical flow, e.g. Benosman, Clercq, Lagorce, Ieng, and Bartolozzi (2014), Benosmana, Ieng, Clercq, Bartolozzi, and Srinivasan (2012), Brosch, Tschechne, and Neumann (2015), Haessig, Cassidy, Alvarez, Benosman, and Orchard (2018) , and visual tracking, e.g. Zhang et al. (2022). However, little has been done on building biological visual systems based on ON/OFF channels. The connection between the proposed ON/OFF-channel-based models and DVS should be strengthened. The efficacy of the proposed methods in DVS should also be investigated. A method based on dynamic vision sensor was proposed to report pixel polarity events including ON-event and OFF-event for sensing OF on a mobile robot, and compared with the traditional EMD for collision avoidance (Milde, Bertrand, Benosmanz, Egelhaaf, & Chicca, 2015). Another latest work reported a neuromorphic model as collision avoidance network in DVS, via the modelling of ON/OFF spiking neural network (Schoepe et al., 2021); this contributed a closed-loop system to deepen our understanding of processing in neural networks and their computations in both biological and artificial systems. In general, the event-based visual sensing strategies would be a promising future trend for motion perception, and the ON/OFF channels are a perfect match to DVS.

Potential for machine learning. Machine learning has led dramatic success in AI applications, and increasing expectations for autonomous systems that exhibit biological/human intelligence. These expectations, however, confront fundamental obstacles that cut across many AI application areas. One such obstacle is explainability or interpretability, also widely known as the machine learning "black box". The models cannot explain reasons behind their predictions or recommendations, hindering diagnosis. For example, deep neural networks can handle with a variety of visual tasks like object detection and recognition very well. The intermediate layers, however, are uninterpretable as their representations. Another obstacle would be adaptability or robustness, which indicates the capability of models to react to or recognise new circumstances they have not been specifically programmed or trained for.

In this regard, the bio-plausible computation has great potential for improving both interpretability and adaptability, which could be an alternative solution to current challenges faced by machine learning in computer vision and robotics. Incorporating prior knowledge from neuroscience, the visual systems or neural networks can be formulated with indicative, organisational, and functional building blocks to reduce the feature dimension for training and, to some extent, increase the explainability. For instance, the fly visual systems have rigorous arrangements of neuropile layers for preliminary motion processing, which unravel the internal network structure generic to other insect-inspired modelling works, e.g. Fu, Li, and Peng (2022). The ON/OFF EMD models implement different correlation of motion detectors that are highly structured to generate DS in motion perception (Borst & Egelhaaf, 1989; Egelhaaf et al., 1989). Each pairwise detectors can share same parameters accounting for physiological and behavioural responses. The "black box" thus becomes partially transparent via introducing bio-plausible pathways and mechanisms.

Biological visual systems have evolved to be highly adaptive to input signal variability. Previous sections have presented the motion perception models based on ON/OFF channels show satisfactory robustness coping with different visual tasks. More specifically, the ON/OFF LPTC models can perceive directional foreground translating OF against moving cluttered backgrounds (Fu & Yue, 2017b, 2020b). The ON/OFF LGMD models work effectively to predict imminent collision dangers in different dynamic environments (Fu, Hu et al., 2020; Fu, Hu, Peng et al., 2018; Fu et al., 2021). The ON/OFF STMD models demonstrate robustness of discriminating between small moving targets and fake motions in cluttered dynamic backgrounds (Bagheri, Wiederman et al., 2017; Wang, Peng, Zheng & Yue, 2020). Avoiding segmentation, registration, classification based methods, such motion perception models are advantageous in simple structure of feed-forward visual processing. Their performance can compete with, or even outperform state-of-the-art machine learning based computer vision methods for motion detection. The ON/OFF channels are a new paradigm to be associated with machine learning methods for developing new classification or recognition systems.

8.3. Hypothesis back to neuroscience

Can bio-inspired computations and bionic applications, all of which take inspiration from biological systems and behaviours, provide useful implications or hypotheses back to neuroscience? The answer is definitely "Yes". Two decades ago, Webb reflected with the impact of robotic research including bio-inspired vision on investigations of animals' behaviour (Webb, 2000, 2001). Webb proposed that bio-robotic studies could be good paradigms for studying animals' behaviours. More recently, a *Science* paper (Webb, 2020) gave insights into bio-robotic implementation of neural models including the ESTMD (Bagheri, Cazzolato et al., 2017), which can play a role of focusing on understanding functional neural circuits corresponding to successful behaviour, such as target tracking. Besides, Chen et al. recommended that neuro-robots can be a powerful means towards understanding neuro-ethology, and provide methodologies for explainable AI and machine learning (Chen et al., 2020). In addition, a *Nature* paper also strongly supported the idea of bringing together AI and neuroscience to yield benefits for each other (Savage, 2019). The author presents a few excellent paradigms to show AI methods analogous to brains on the aspects of dealing with data, reproducing senses, and learning.

When progressing neuroscience on brain's signal processing, large parts of anatomy and physiology remain elusive, although new techniques like neurogenetic methods have been gradually developed to provide precise control over the activity of individual neurons. While biological substrates and behaviours are not fully unravelled, bio-plausible computations and bio-robotic approaches are of particular usefulness to simulate biological systems and behaviours, yield implications or hypotheses. Animals are studied to improve computer models by copying the brain's processes; in parallel, computational and robotic implementations allow these models to be tested in real bodies interacting with real environments. I argue that such bio-plausible research paradigm (see **Fig. S6**) can strengthen the interplay between neuroscience, computer science, and machine intelligence for innovating AI technology. To draw the attention upon ON/OFF channels, some instances herein are given to show how the different disciplines can influence positively each other.

As mentioned in Section 4, the fly visual systems are widely acknowledged as prominent paradigms to study motion perception. There are different combinations of ON/OFF channels implementing the classical EMD in early visual processing pathways, i.e., 2-Q, and 6-Q computational structures. The debate for either form of ON/OFF EMD in fly visual systems stimulated neuroscientists to further investigate the internal neural structures 定从 underlying motion vision (Joesch et al., 2013). In addition to that, the 6-Q computational model that resembles the behavioural response of fruit fly *Drosophila* argued interactions between ON/OFF channels (Clark et al., 2011), controversial to the vast majority of views on encoding motion in parallel ON/OFF channels (Borst et al., 2020; Eichner et al., 2011; Gabbiani & Jones, 2011; Joesch et al., 2010). Furthermore, there are neural mechanisms such as feedback contrast mediation (Bahl, Serbe, Meier, Ammer, & Borst, 2015), lateral inhibition interneurons LPi (Mauss et al., 2015), visual projection neurons like LPLC2 located deeper in the brain not fully understood or explored. The corresponding neural modelling that realises similar DS or functionality (Drews et al., 2020; Fu & Yue, 2020b, 2021) could propagate meaningful information back to neuroscience, and even validate underlying neural structures and mechanisms in motion perception.

Regarding visual tracking, STMD neurons in dragonflies have been replicated into a wheeled robot platform performing active pursuit (Bagheri, Cazzolato et al., 2017). This for the first time offered insights into the neural mechanisms underlying small target detection, tracking, and pursuing via the robot's responsive actions such as "saccade" , a quick movement to align target centred in RF. The researchers applied the well-established ESTMD model to emulate a biological process of "facilitation" , that is, a slow build-up of activity of moving targets on consistent trajectories confined in RF. This work formulated a closed-loop activity from perception to actuation which efficiently improves tracking performance in the presence of visual clutter and distractors, even outperforming state-of-the-art computer vision algorithms in visual tracking.

Another instance shows the computational modelling of ON/OFF translating perception neural network to mimic the fly motion tracking and fixation behaviour. A *Nature* paper (Bahl et al., 2013) revealed the fast visual tracking in *Drosophila* is co-mediated by two neural pathways, i.e., a motion pathway implementing an array of classical EMD models corresponding to optomotor response, and a position pathway quickly indicating the locational information of moving targets within the field of vision. For extending the neuroscience study and verifying its main findings, the authors in Fu, Bellotto et al. (2018), Fu and Yue (2017a) showed bio-plausible computation and micro-robot implementation of T4 (ON) and T5 (OFF) pathways towards the closed-loop fixation behaviour in real environment. Besides, a biological finding was validated whereby the position pathway alone is capable of directing fixating response; whilst the ON/OFF motion pathway can improve the tracking accuracy by reactive turning response.

Basically, the tracking behaviour is hard to analyse through either physiological or ethological experiments on real insects. The aforementioned two embodiments of insect's visual tracking in autonomous robots could also explain selective attention responses observed in downstream neurons (Lancer, Evans, Fabian, O'Carroll, & Wiederman, 2019). Hence, the neural model implemented on robot allows neural data collected from immobilised insect to be understood, in the context of robot imitation under a closed-loop control from perception to motion.

Compared to fly visual systems, there is quite a smaller number of physiological studies in support of the existence of ON/OFF channels in the pre-synaptic neural circuits of LGMD neurons (Jones & Gabbiani, 2010; O'Shea & Rowell, 1976; O'Shea & Williams, 1974; Osorio, 1987, 1991; Peron et al., 2009). Despite that, the characteristic differences between LGMD-1 and LGMD-2 boosted the modelling of parallel ON/OFF channels in the LGMD neural network models by borrowing concepts from fly physiology, in order to separate the functionality and selectivity (Fu, Hu et al., 2020; Fu, Hu, Peng et al., 2018). Through modelling biased-ON/OFF channels for parallel visual computation, the specific selectivity of LGMD-2 to only OFF-contrast looming stimuli, i.e., motion induced by darker object approaching, is fulfilled with corroboration in both computational and micro-robotic implementations (Fu, Hu et al., 2020). These bio-plausible modelling works thus provided hypothesis that the ON/OFF channels play roles in the locust's visual brain.

9. Conclusion

This paper has introduced the advantages and uniqueness of ON/OFF channels in constructing motion perception models to address real world challenges. By gathering perspectives from neuroscience, computer science and engineering, this paper has elaborated on (1) why biological visual systems evolve to process motion information in parallel pathways, (2) how signal bifurcation is implemented and the ON/OFF motion signals are delivered, correlated to generate different selectivity in motion perception. Most importantly, the benefits of ON/OFF channels facilitating different motion perception tasks have been elucidated from the perspective of neural modelling. This research has surveyed comprehensively on relevant neuroscience milestones, mathematical/computational models and applications in current literature, and provides in-depth studies to demonstrate the efficacy of ON/OFF channels to solve typical motion perception problems. Specifically, three categories of neural models, i.e., EMD, LGMD, STMD based on ON/OFF channels have been presented and investigated. Their machine vision applications have also been summarised. At last, this paper has discussed on challenges, future trends upon ON/OFF channels with connection to bio-inspired sensors and machine learning, as well as hypotheses back to neuroscience, all together, aiming at developing robust artificial vision systems and sensor strategies, closing the gap between biological and artificial lives.

ON/OFF channels are ubiquitous amongst animals in nature, a governing principle for creating selectivity in motion perception. I argue that for building dynamic vision systems, one should not simply apply existing computer vision algorithms or follow routine deep learning methods, but exploit insights from natural intelligence to pursue efficient AI.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

No data was used for the research described in the article.

Acknowledgements

This research has received funding from the Social Science Fund of the Ministry of Education of China under the Grant No. 22YJCZH032, the National Natural Science Foundation of China under the Grant No. 12031003, No. 12211540710, and the European Union's Horizon 2020 ULTRACEPT project under the Grant No. 778062.

Appendix A. Supplementary data

Supplementary material related to this article can be found online at https://doi.org/10.1016/j.neunet.2023.05.031.

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