Area MT+ in Human Brain Responsible for Optic Flow Processing

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ABSTRACT
Optic flow — the dynamic light motion pattern that projects on moving observers’ retina — plays great roles in many behaviors. Huge neurophysiological and neuroimaging studies have been conducted to reveal the cortical areas in human brain that respond to optic flow. One of the most important cortical areas is area MT+ (MT & MST). In the current paper, I tried to summarize the previous studies about human area MT+ and pointed out their existing questions. Based on these questions, I proposed several future research directions. Solving these questions will improve our understanding about the role of area MT+ in optic flow processing.

Keywords: MT+, MST, MT, human brain, optic flow

1. INTRODUCTION
When observers are moving in the environment, the objects in the environment would project on observers’ retina and generate a dynamic motion pattern named as optic flow. This concept was first introduced by James J. Gibson (1950), an American psychologist. Optic flow contains rich information, such as the 2D structure information – focus of expansion (FoE) and the 3D structure information, e.g., speed gradient or motion parallax (e.g., Koenderink, 1986; Longuet-Higgins & Prazdny, 1980).

According to the definition of optic flow, it is clear that optic flow is generated by our self-movements. In our daily life, the self-movements are various. For example, while walking on a street, we would like to move straight forwards or rotate our eyes while moving to become familiar with the surroundings. Sometimes, we would move back to avoid from hitting obstacles. Therefore, the optic flow can be presented in various forms. Specifically, moving straight forward generates radial expansion optic flow (Figure 1a); moving straight backward generates radial contraction optic flow (Figure 1b); if we rotate at a fixed position, a rotation optic flow would be generated (Figure 1c). Of course, sometimes we would laterally move which generates a translation optic flow (Figure 1d). These types of optic flow are generally simple, because they are generated by simple movements. Most of the time in our daily life, our self-movements are complex. For example, we tend to move forward and rotate our eyes to observe the environment, simultaneously. In this situation, a complex spiral expansion optic flow would be generated that is the combination of expansion radial and rotation optic flow (Figures 1e and 1f).

Figure 1. Different types of optic flow patterns. (a) expansion radial optic flow that is generated when observers are moving straight forward; (b) contraction radial optic flow that is generated when observers are moving straight backward; (c) clockwise rotation optic flow that is generated when observers are rotating around the vertical axis clockwise; (d) translation optic flow that is generated when observers are moving laterally to the left or right; (e) expansion clockwise spiral optic flow that is generated when observers are moving straight forward and rotating clockwise; (f) contraction clockwise spiral optic flow that is generated when observers are moving backward and rotating clockwise. This figure was from Sun (2021).
Additionally, thousands of studies have been conducted and revealed that optic flow plays great roles in many behaviors, such as control of stance (Lim et al., 2018; Piras et al., 2018) and speed (Baumberger et al., 2000; Petto & Chatziastros, 2006; Prokop et al., 1997), perception of spatial depth (Li et al., 2016; Simpson, 1993; Wexler & Van Boxtel, 2005)) and path (Li & Cheng, 2011; Raudies & Neumann, 2013; Warren et al., 1991), and the heading (i.e., self-motion direction) perception (Li et al., 2002; Sun et al., 2020; van den Berg, 1992; Warren et al., 2001).

Because of the diversity and the importance of optic flow in our daily behaviors, the neural bases of the optic flow processing attract many researchers’ interest. Since now, many cortical areas in human brains have been revealed in the processing of optic flow, e.g., V3a (Bartels et al., 2008; Cardin et al., 2012; Fischer et al. 2012; Kuai et al., 2020; et al., 2013; Strong et al., 2017; Wall et al., 2008; Wall & Smith, 2008), V3b/KO (Dupont et al., 1997; Kuai, et al., 2020; Wall & Smith 2008), V7 (Cardin et al., 2012; Ohlendorf et al., 2008), MT+ (MT, MST) (Dukelow et al., 2001; Morrone et al., 2000; Wall et al., 2008), VIP (Field et al., 2020; Furlan et al., 2014; Pitizalis et al., 2013; Wall & Smith, 2008), CSv (Field et al., 2015; Furlan et al., 2014; Wall & Smith, 2008; Pitizalis et al., 2013), and p2vc (Fischer et al., 2012; Furlan et al., 2014; Furlan & Smith, 2016; Pitizalis et al., 2013). In the current article, I mainly reviewed the studies focusing on the area MT+, and proposed the future research direction for the area MT+.

2. AREA MT+ (MT AND MST) IN HUMAN BRAIN

Previous studies with the help of PET, histological and fMRI techniques have revealed that area MT+ in the human brain is similar to area MT+ in the monkey brain.

Morrone et al (2000) first divided human MT+ into MST and MT based on their selectivity to the motion patterns. Specifically, area MT tends to respond to the translation 2D global motion patterns, while area MST prefers to respond to the rotation and radial 2D global motion. However, Wall et al (2008) set up an experiment and found some different results. In their experiment, they showed two patterns to the observers while monitoring the BOLD signal using the fMRI techniques. The patterns they presented to the observers were either the same (both are radial or rotation) or different (radial vs. rotation). The results showed that both radial and rotation motion patterns elicited higher BOLD signals suggesting that areas MT and MST in the human brain respond to both the radial and rotation motion patterns.

Dukelow et al (2001) divided MT+ area into MT and MST based on their different receptive visual field features. To be more specific, they discovered that area MT was stimulated by the motion patterns presented in the contralateral visual field. By contrast, area MST responds to the motion patterns presented in both the contra and ipsilateral visual fields. For example, area MT in the left brain prefers to be activated by the motion stimuli in the right eye, but area MST prefers to be activated by the motion stimuli in both eyes. This finding is generally accepted and is always used to locate area MT and area MST in a human brain now (also see Huk, et al., 2002).

3. QUESTIONS IN THE PREVIOUS STUDIES

When I was reviewing the previous studies about the area of MT+ in the human brain, I found several questions. First of all, some studies generally took 2D motion patterns as optic flow (e.g., Dukelow et al., 2001; Greenlee, 2000; Giaschi et al., 2007; Koyama et al., 2005; Pitizalis et al., 2010; Rutschmann et al., 2000; Smith et al., 2006; Strong et al., 2017; Wall et al., 2008; Wall & Smith, 2008; Uesaki & Ashida, 2015). However, optic flow and 2D motion patterns are different. Specifically, optic flow is the projection of objects as we are moving in the world and containing rich 3D structure information, such as motion parallax or speed gradient (for example, Koenderink, 1986; Longuet-Higgins & Prazdny, 1980). However, 2D motion pattern is one kind of global motion pattern in which all dots are randomly positioned on a vertical plane and move with a constant speed or a constant acceleration. In this case, no speed gradient or motion parallax is in 2D motion pattern, which means that no 3D information was provided to the observer. However, so far, the activities of area MT+ to 2D global motion patterns and optic flow stimuli were tested separately, i.e., there was no single study in which 2D motion patterns and optic flow stimuli were tested simultaneously, leading to the question: whether the brain areas that respond to optic flow and 2D global
motion patterns show unique responses specific to optic flow stimuli.

Additionally, some human-fMRI studies found that area MT+ in the human brain responds to different types of motion patterns differently (Giaschi et al., 2007; Strong et al., 2017; Wall et al., 2008); while some studies found that area MT+ could not do it (Pitzalis et al., 2013). This might due to the former studies adopted a more sophisticated data analysis method, i.e., MVPA analysis; whereas, the other studies only conducted the simple GLM analysis. Compared with GLM analysis, MVPA could reveal the pattern differences between different experimental conditions or stimuli. The different results due to the different data analysis methods lead to the problem of whether human MT+ could differentiate different optic flow patterns remains unclear.

Furthermore, neurophysiological studies (e.g., intracranial electrode technology) have recorded the activities of signal neurons to different types of optic flow and the 2D motion pattern (e.g., Duffy & Wurtz, 1991a, 1991b), and the information in the motion stimuli (Duffy & Wurtz, 1997), but no human study investigate that how the individual neurons in area MT+ of human brain respond to optic flow and 2D motion patterns, and the information in the motion stimuli.

Lastly, recent studies about the heading perception with optic flow proposed that heading perception is consistent with the Bayesian account, meaning that the perceived heading biased toward the prior information (e.g., Xing & Saunders, 2016). Recent monkey neurophysiological studies have figure out the distribution of prior information with intracranial electrode technology (Gu et al., 2010). By contrast, the prior information used by human participants is still on the theory.

4. FUTURE DIRECTIONS

With the above-mentioned problems in the previous studies, the future work can focus on the following questions:

A series of studies should be conducted in which optic flow and 2D motion patterns can be simultaneously examined so that we can figure out whether the neural basis of 2D motion pattern and optic flow different or not. If they are different, then we can prove the specificity of optic flow processing.

Meanwhile, a more direct research method, e.g., intracranial electrode technology (Campbell & Wu, 2018), can be applied to the human participants. With this kind of research technology, we can directly reveal the activity features of the human MT+ area to optic flow and solve the disputes because of different data analysis methods.

Furthermore, in the future, with the help of the intracranial electrode technology, we can directly examine whether the neural activities of human MT+ can be modulated by the 3D structure information, e.g., speed gradient. Solving this problem not only helps us reveal the homogeneity of the monkey brain and human brain, but also provides evidence for the specificity of optic flow processing.

Importantly, intracranial electrode technology can also reveal the distribution and selectivity of different MT+ neurons. With the signal neuron data, we can figure out the prior information that we used to modulate our heading perception, providing evidence for the Bayesian account of heading perception.

5. CONCLUSIONS

In the current paper, I reviewed the studies about the area MT+ (MST and MT) in human brains. I listed the research questions in the previous studies and provided several research directions to our following researchers. After answering the above questions, we can have a better understanding of optic flow processing, and provide powerful evidence for a long-existing dispute in the area of visual perception and action: what we see is 2D motion pattern or optic flow.

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