Annals of Mathematics **174** (2011), 1219–1241
http://dx.doi.org/10.4007/annals.2011.174.2.11

Representation theoretic patterns in three dimensional Cryo-Electron Microscopy I: The intrinsic reconstitution algorithm

By Ronny Hadani and Amit Singer

Abstract

In this paper, we reveal the formal algebraic structure underlying the intrinsic reconstitution algorithm, introduced by Singer and Shkolnisky in [9], for determining three dimensional macromolecular structures from images obtained by an electron microscope. Inspecting this algebraic structure, we obtain a conceptual explanation for the admissibility (correctness) of the algorithm and a proof of its numerical stability. In addition, we explain how the various numerical observations reported in that work follow from basic representation theoretic principles.

0. Introduction

The goal in cryo-EM is to determine three dimensional macromolecular structures from noisy projection images taken at unknown random orientations by an electron microscope, i.e., a random Computational Tomography (CT). Determining three dimensional macromolecular structures for large biological molecules remains vitally important, as witnessed, for example, by the 2003 Chemistry Nobel Prize, co-awarded to R. MacKinnon for resolving the three dimensional structure of the Shaker K+ channel protein [2], [7], and by the 2009 Chemistry Nobel Prize, awarded to V. Ramakrishnan, T. Steitz and A. Yonath for studies of the structure and function of the ribosome. The standard procedure for structure determination of large molecules is X-ray crystallography. The challenge in this method is often more in the crystallization itself than in the interpretation of the X-ray results, since many large proteins have so far withstood all attempts to crystallize them.

Cryo-EM is an alternative approach to X-ray crystallography. In this approach a sample of identical macromolecules are rapidly immobilized in thin layer of vitreous ice. The cryo-EM imaging process produces a large collection of tomographic projections, corresponding to different and unknown orientations of the various molecules in the solution. The intensity of the pixels in a projection image are correlated with the integrals along lines which are parallel to the viewing direction (see Figure 1). The goal is to reconstruct the three

dimensional structure of the molecule from such unlabeled projection images. The principal difficulty is that the highly intense electron beam destroys the molecules and it is therefore impractical to take projection images of the same molecule at known different directions as in the case of classical CT. In other words, a single molecule can be imaged only once, rendering an extremely low signal-to-noise ratio (SNR), mostly due to shot noise induced by the maximal allowed electron dose.

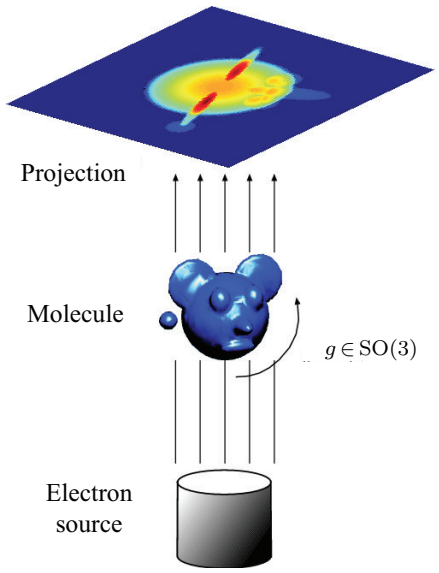

Figure 1. Schematic drawing of the imaging process: every projection image corresponds to some unknown spatial orientation of the molecule.

Three dimensional reconstruction from Cryo-EM images is of particular interest because it promises to be an entirely general technique that does not require crystallization or other special preparation stages; it is beginning to reach sufficient resolution to allow the trace of polypeptide chains and the identification of residues in protein molecules [5], [6], [13].

Over the years, several methods have been proposed for three dimensional reconstruction from cryo-EM images. Present methods are based on the "Angular Reconstitution" algorithm of Van Heel [12], also developed independently by Vainshtein and Goncharov [3]. However, these methods fail in many situations of practical interest when the molecules are too small, the cryo-EM images are too noisy or at resolutions where the signal-to-noise ratio becomes too small.

0.1. *Mathematical model.* Instead of thinking of a multitude of molecules immobilized in different orientations and observed by a microscope held in a fixed position, it is more convenient to think of a single molecule, observed by an electron microscope from different viewing directions. Under this convention, the physics of cryo-EM is modeled as follows. Let (V, r) be a three dimensional Euclidean vector space over $\mathbb{R}$, where $r : V \times V \to \mathbb{R}$ is the Euclidean inner product.

- The molecule is modeled by a real valued function $\phi : V \to \mathbb{R}$, which describes the electric potential due to the charge density in the molecule.
- The viewing direction of the electron microscope is modeled by a point x on the unit sphere $X = S(V)$.
- The projection image obtained by the microscope, when observing the molecule from a viewing direction x is a real valued function R_x on the orthogonal plane $\mathrm{P}_x = x^{\perp}$, given by the X-ray projection of the potential ϕ along the viewing direction,

$$R_x(v) = \mathrm{Xray}_x(\phi)(v) = \int_{L_x} \phi(v + l)\, dl$$

for every $v \in \mathrm{P}_x$, where L_x is the line passing through x and dl is the Euclidean measure on L_x.

The data collected from the experiment is a set of projection images $\{R_x : \mathrm{P}_x \to \mathbb{R},\ x \in X_N\}$, where $X_N \subset X$ is a subset consisting of N points. A standard assumption is that the points $x \in X_N$ are distributed independently and uniformly at random on the unit sphere X. This corresponds to the empirical assumption that the orientations of the molecules in the solution are uniformly distributed. In addition, we assume that the function ϕ is generic in the sense that each projection image is associated with a unique viewing direction. In particular, this assumption implies that the molecule admits no nontrivial symmetry.

It is important to emphasize that the viewing direction associated with every projection image is not known; thus, the vector space P_x is only given as an abstract vector space, and the main problem of cryo-EM is to reconstruct the orthogonal embedding $i_x : \mathrm{P}_x \hookrightarrow V$ associated with every label $x \in X_N$. We will refer to this problem as the *cryo*-EM *reconstruction problem* and note that, granting its solution, the potential function ϕ can be computed (approximately) using the inverse X-ray transform.

0.2. *Main results.* In [9], a novel algorithm for solving the cryo-EM reconstruction problem for the case the potential ϕ is generic was presented; in this paper it is referred to as *the intrinsic reconstitution algorithm.* It has

the appealing property of exhibiting remarkable numerical stability to noise. Although the admissibility (correctness) and the numerical stability of this algorithm were verified in a large number of numerical simulations, a formal justification was still missing.

In this paper, we reveal the formal algebraic structure underlying the intrinsic reconstitution algorithm. Inspecting this structure, we obtain a conceptual explanation for the admissibility (correctness) of the algorithm and a proof of its numerical stability. The analysis relies on studying the spectrum of a certain operator C, of geometric origin, referred to as the *common lines operator*. Specifically,

- admissibility amounts to the existence of a *canonical* isometry between the Euclidean vector space V and the eigenspace of C associated with the maximal eigenvalue;
- numerical stability amounts to the existence of a *spectral gap* that separates the maximal eigenvalue of C from the rest of the spectrum.

In this regard, the main technical result of this paper is a complete description of the spectrum of the common lines operator in terms of representation theory of the orthogonal group. In the course of our presentation, we explain how the various numerical observations reported in [9] follow from basic representation theoretic principles, thus putting that work on firm mathematical grounds.

Finally, we note that the algebraic constructions presented in this paper were further developed in [4] and [10], as part of a novel algorithm for *class averaging*, which is another difficult fundamental problem in cryo-EM. We hope that further elaboration will also enable us to generalize the intrinsic reconstitution algorithm to the case of nongeneric potentials, such as the ones that are associated with symmetric molecules. This important development will be studied in a future publication.

The remainder of the introduction is devoted to a detailed description of the intrinsic reconstitution algorithm and to the explanation of the main ideas and results of this paper.

0.3. *The Fourier slicing property and the common lines datum.* The first step of the algorithm is to extract from the projection images a linear algebra datum that captures a basic relation in three dimensional Euclidean geometry, referred to as *the common lines datum*. The extraction uses a basic property of the Fourier transform, called the *Fourier slicing property* (see [8]), asserting that

$$\widehat{\mathrm{Xray}_x(\phi)} = \widehat{\phi}|\mathrm{P}_x \tag{0.1}$$

for every $x \in X$, where the operation $\widehat{(-)}$ on the left-hand side denotes the Euclidean Fourier transform on the plane P_x and the operation $\widehat{(-)}$ on the right-hand side denotes the Euclidean Fourier transform on V. Equation (0.1)

is equivalent to the well-known fact that the Fourier transform interchanges restriction with integration.

The key observation, first made by Klug (see [1]), is that (0.1) implies, for every pair of distinct points $x, y \in X_N$, that the functions $\widehat{R}_x$ and $\widehat{R}_y$ must agree on the line of intersection (common line); that is

$$\widehat{R}_x | \mathrm{P}_x \cap \mathrm{P}_y = \widehat{R}_y | \mathrm{P}_x \cap \mathrm{P}_y.$$

This means that for a generic function ϕ, one can compute from the functions $\widehat{R}_x$ and $\widehat{R}_y$ the linear map $C_N(x,y) : \mathrm{P}_y \to \mathrm{P}_x$, that identifies the line of intersection between the two planes (at least to some approximation). Formally, this map is given by the composition of $C_{x,y} \circ C_{y,x}^t$, where $C_{x,y}$ and $C_{y,x}$ are the tautological embeddings

$$C_{x,y} : \mathrm{P}_x \cap \mathrm{P}_y \hookrightarrow \mathrm{P}_x,$$
$$C_{y,x} : \mathrm{P}_x \cap \mathrm{P}_y \hookrightarrow \mathrm{P}_y.$$

In the case the point $x = y$, one defines the common line map $C_N(x,y)$ to be the zero mapping.

0.4. *The intrinsic reconstitution algorithm.* The algorithm accepts, as an input, the common lines datum $\{C_N(x,y) : (x,y) \in X_N \times X_N\}$ and computes, as an output, the orthogonal embedding $i_x : \mathrm{P}_x \to V$ associated with every label $x \in X_N$, up to some unique global orthogonal transformation of V. In more precise terms, the output is a set of orthogonal embeddings $\varphi_x : \mathrm{P}_x \to V$, $x \in X_N$ such that $\varphi_x = g \circ \iota_x$ for every $x \in X_N$, where g is an element of the full orthogonal group[1] $O(V)$ which does not depend on the label x.

The crucial step is to construct an *intrinsic* model of the three dimensional Euclidean vector space V, expressed solely in terms of the common lines datum.

The algorithm proceeds in four steps.

(1) *Ambient vector space.* Consider the $2N$ dimensional Euclidean vector space
$$\mathcal{H}_N = \bigoplus_{x \in X_N} \mathrm{P}_x,$$
where vectors $s \in \mathcal{H}_N$ are N-tuples indexed by elements of X_N: $s = (s(x))_{x \in X_N}$, with each $s(x) \in P_x$. The Euclidean structure on $\mathcal{H}_N$ is induced from the one on each of its component.

(2) *Common lines operator.* Consider the linear operator $C_N : \mathcal{H}_N \to \mathcal{H}_N$, given by
$$C_N(s)(x) = \frac{1}{N} \sum_{y \in X_N} C_N(x,y)\, s(y).$$

[1]As a consequence, the left/right-handedness of the molecule is not retrieved by the algorithm.

The operator C_N is symmetric since $C_N(x,y) = C_N(y,x)^t$ for every $x, y \in X_N$.

(3) *Intrinsic vector space.* Compute the vector space $\mathbb{V}_N \subset \mathcal{H}_N$, given by[2]

$$\mathbb{V}_N = \bigoplus_{\lambda > 1/3} \mathcal{H}_N(\lambda),$$

where $\mathcal{H}_N(\lambda)$ denotes the eigenspace of C_N associated with the eigenvalue λ. The vector space $\mathbb{V}_N$ admits a Euclidean structure, induced from that of $\mathcal{H}_N$.

(4) *Intrinsic maps.* For every label $x \in X_N$, compute the map

$$\varphi_x = \sqrt{2/3} \cdot \mathrm{pr}_x^t : \mathrm{P}_x \to \mathbb{V}_N,$$

where $\mathrm{pr}_x : \mathbb{V}_N \to \mathrm{P}_x$ is the restriction to $\mathbb{V}_N$ of the orthogonal projection from $\mathcal{H}_N$ onto its x-th component.

THEOREM 1. *For sufficiently large N, we have*

$$\dim \mathbb{V}_N = 3.$$

To conclude, the output of the algorithm is a pair consisting of a three dimensional Euclidean vector space $\mathbb{V}_N$ and a linear map $\varphi_x : \mathrm{P}_x \to \mathbb{V}_N$, associated with every label $x \in X_N$. The fact that this data establishes a solution to the cryo-EM reconstruction problem is the content of the following theorem.

THEOREM 2. *There exists an (approximate) isometry $\tau_N : V \approx \mathbb{V}_N$ which satisfies the following property*:

$$\tau_N \circ i_x = \varphi_x$$

for every $x \in X_N$.

Remark 1. Theorem 2 implies that the vector space V equipped with the tautological embeddings $\{i_x : \mathrm{P}_x \to V,\ x \in X_N\}$ is isomorphic, as a Euclidean vector space, to the intrinsic vector space $\mathbb{V}_N$ equipped with the mappings $\{\varphi_x : \mathrm{P}_x \to \mathbb{V}_N,\ x \in X_N\}$. Hence, the latter set determines the former up-to a unique global orthogonal transformation of V. The precise statement of Theorem 2 is given in Theorem 6, which appears in the body of the paper.

0.5. *Continuous limit.* The proofs of Theorems 1 and 2 are based on considering the "continuous limit" of the algorithm, by taking the number of projection images $N \to \infty$. In the limit,

- the finite configuration space X_N converges to the unit sphere X;

[2]The condition $\lambda > 1/3$ in the definition of $\mathbb{V}_N$ will be clarified when we discuss the spectral gap property in the next subsection.

- the ambient Euclidean vector space $\mathcal{H}_N$ converges to an infinite dimensional Euclidean vector space $\mathcal{H}$;
- the common lines operator $C_N : \mathcal{H}_N \to \mathcal{H}_N$ converges to a symmetric integral operator $C : \mathcal{H} \to \mathcal{H}$; .
- the intrinsic model $\mathbb{V}_N$ converges to the eigenspace of C, associated with the maximal eigenvalue.

The vector space $\mathcal{H}$ consists of smooth global sections of the vector bundle $\mathfrak{H} \to X$, whose fiber at a point $x \in X$ is the plane $\mathrm{P}_x = x^{\perp}$, with the Euclidean structure given by

$$(s_1, s_2) = \int\limits_{x \in X} r\left(s_1\left(x\right), s_2\left(x\right)\right) dx,$$

where dx is the Haar measure on the unit sphere. The integral operator $C : \mathcal{H} \to \mathcal{H}$ is given by

$$C\left(s\right)\left(x\right) = \int\limits_{y \in X} C\left(x, y\right) s\left(y\right) dy,$$

where $C\left(x, y\right) : y^{\perp} \to x^{\perp}$ is the common line map associated to the pair of points $x, y \in X$. In addition, the vector space $\mathcal{H}$ carries an action of the orthogonal group $O\left(V\right)$, preserving the Euclidean structure, and the operator C commutes with the group action. Consequently, the spectrum of C can be interpreted in terms of the representation theory of the orthogonal group. Based on this interpretation, we derive the first main result of this paper.

THEOREM 3. *The operator C admits a kernel and a discrete nonzero real spectrum $\lambda_n \in \mathbb{R}$, $n \in \mathbb{N}$, such that*

$$\lambda_n = \frac{(-1)^{n-1}}{n\left(n+1\right)}.$$

Moreover, $\dim \mathcal{H}\left(\lambda_n\right) = 2n + 1$.

An immediate implication of Theorem 3 is that the maximal eigenvalue of C is $\lambda_{\max} = 1/2$, its multiplicity is equal 3 and there exists a *spectral gap* of $\lambda_1 - \lambda_3 = 5/12$, which separates it from the rest of the spectrum. Let us define, for every point $x \in X$, the map

$$\varphi_x = \sqrt{2/3} \cdot \left(\mathrm{ev}_x | \mathbb{V}\right)^t : \mathrm{P}_x \to \mathbb{V},$$

where $\mathrm{ev}_x : \mathcal{H} \to \mathrm{P}_x$ is the evaluation morphism at the point x. The second main result of this paper is:

THEOREM 4. *There exists a canonical isomorphism of Euclidean vector spaces $\tau : V \to \mathbb{V}$, satisfying*

$$\tau \circ i_x = \varphi_x$$

for every $x \in X$.

Theorems 1 and 2 follow from Theorem 4.

We end the introduction with the following concluding remark.

Remark 2. The computation of the set of orthogonal embeddings $\{i_x : \mathrm{P}_x \to V,\ x \in X_N\}$ is a nonlinear/nonconvex computational problem because of the orthogonality constraint. Interestingly, the construction of the intrinsic model reduces this problem to a problem in linear algebra, namely, to the computation of the maximal eigenspace of the common lines operator. This computation is numerically stable to noise because of the spectral gap property of the continuous common lines operator in conjunction with an argument from random matrix theory (see [9]). Other existing reconstruction methods, like the angular reconstitution method (see [12] and [3]), do not enjoy this important stability property.

0.6. *Structure of the paper.* The remainder of this paper consists of three sections.

- In Section 1, we begin by introducing the basic analytic set-up which underlies cryo-EM. Then we proceed to formulate the main results of this paper which are: a complete description of the spectral properties of the common lines operator C (Theorem 5) and the admissibility of the intrinsic reconstitution algorithm (Theorem 6).
- In Section 2, we prove Theorem 5; in particular, we develop all the representation theoretic machinery which is needed for the proof.
- Finally, in Appendix A, we give the proofs of all technical statements that appeared in the previous sections.

Acknowledgement. The first author would like to thank Joseph Bernstein for many helpful discussions concerning the mathematical aspects of this work. Also, he would like to thank the MPI institute at Bonn where several parts of this work were concluded during the summer of 2009. We thank Shamgar Gurevich for carefully reading the manuscript and for providing us with various useful remarks. The second author is partially supported by Award Number R01GM090200 from the National Institute of General Medical Sciences. The content is solely the responsibility of the authors and does not necessarily represent the official views of the National Institute of General Medical Sciences or the National Institutes of Health.

1. **Preliminaries and main results**

1.1. *Set up.* Let $O(V) = O(V, r)$ denote the group of orthogonal transformations with respect to the inner product r. Let $\mathrm{SO}(V) \subset O(V)$ denote the subgroup of orthogonal transformations that have determinant one; let $\omega \in O(V)$ denote the element

$$\omega = \begin{pmatrix} -1 & 0 & 0 \\ 0 & -1 & 0 \\ 0 & 0 & -1 \end{pmatrix}.$$

Let $S(V)$ denote the unit sphere in V, that is, $S(V) = \{v \in V : r(v,v) = 1\}$. Finally, we require the following definition.

Definition 1. A pair of points $x, y \in S(V)$ are said to be in *generic position* if $x \neq \pm y$.

1.2. *The vector bundle of planes.* Let $\mathfrak{H} \to S(V)$ be the real vector bundle with fibers $\mathfrak{H}_{|x} = x^{\perp}$ and let $\mathcal{H} = \Gamma(S(V), \mathfrak{H})$ denote the space of smooth global sections. The vector bundle $\mathfrak{H}$ admits a fiberwise Euclidean structure induced from the one on V, which in turns yields a (pre) Euclidean structure on $\mathcal{H}$ (here, the prefix "pre" just means that $\mathcal{H}$ is not complete). In general, in this paper we will not distinguish between a Euclidean/Hermitian vector space and its completion and the correct choice between the two will be clear from the context.

In addition, $\mathfrak{H}$ admits a natural $O(V)$-equivariant structure which induces an action of every element $g \in O(V)$ on the space of global sections $\mathcal{H}$, sending a section $s \in \mathcal{H}$ to a section $g \cdot s$, given by

$$(g \cdot s)(x) = gs\left(g^{-1}x\right) \tag{1.1}$$

for every $x \in S(V)$. The element g on the right-hand side of (1.1) is considered as an invertible linear map from $\left(g^{-1}x\right)^{\perp}$ to $x^{\perp}$. This equivariant structure defines a representation of $O(V)$ on $\mathcal{H}$, preserving the Euclidean structure.

1.3. *The common lines operator.* We proceed to define an integral operator $C : \mathcal{H} \to \mathcal{H}$, referred to as the *common lines operator*. The definition uses the fact that every pair of distinct planes in a three dimensional real vector space must intersect at a line. In more precise terms, for every pair of points $x, y \in S(V)$ in generic position, there are two tautological embeddings of the intersection line $x^{\perp} \cap y^{\perp}$ between the corresponding orthogonal planes

$$C_{x,y} : x^{\perp} \cap y^{\perp} \hookrightarrow x^{\perp},$$
$$C_{y,x} : x^{\perp} \cap y^{\perp} \hookrightarrow y^{\perp}.$$

We use these embeddings to define a rank one linear map $C(x,y) : y^{\perp} \to x^{\perp}$, given by the composition

$$C(x,y) = C_{x,y} \circ C_{y,x}^{t}.$$

The collection $\{C(x,y) : x, y \in X \text{ in generic position}\}$ defines a distribution section of $\mathfrak{H} \boxtimes \mathfrak{H}^{*}$, smooth on the complement of the union of the diagonal and the anti-diagonal, thus establishing a kernel of an integral operator $C : \mathcal{H} \to \mathcal{H}$, given by

$$C(s)(x) = \int_{y \in S(V)} C(x,y)\, s(y)\, dy$$

for every $s \in \mathcal{H}$, where dy is the normalized Haar measure on the sphere. The common lines operator satisfies the following properties.

(1) It is symmetric; namely, $C = C^t$.
(2) It commutes with the $O(V)$-action; namely, $C(g \cdot s) = g \cdot C(s)$ for every $s \in \mathcal{H}$ and $g \in O(V)$.

The first property follows from the fact that $C(x,y) = C(y,x)^t$ for every $x, y \in S(V)$ in generic position. The second property follows from the fact that

$$C(gx, gy) = g \circ C(x,y) \circ g^{-1} \tag{1.2}$$

for every $x, y \in S(V)$ in generic position and every element $g \in O(V)$. In the right-hand side of (1.2) we consider the element g as an invertible linear map from $x^\perp$ to $(gx)^\perp$ and the element g^{-1} as an invertible linear map from $(gy)^\perp$ to $y^\perp$.

1.4. *Intrinsic model.* Our goal is to describe a Euclidean vector space $\mathbb{V}$, which is defined solely in terms of the common lines operator and the Euclidean structure on $\mathcal{H}$, and is canonically isomorphic to the Euclidean vector space V. The vector space $\mathbb{V}$ is referred to as the *intrinsic* model of V. As a preliminary step, we provide a complete description of the spectrum of the common lines operator.

THEOREM 5. *The operator C admits a kernel and a discrete nonzero real spectrum $\lambda_n \in \mathbb{R}$, $n \in \mathbb{N}$, such that*

$$\lambda_n = \frac{(-1)^{n-1}}{n(n+1)}.$$

Moreover, $\dim \mathcal{H}(\lambda_n) = 2n+1$.

For a proof, see Section 2.

We define the intrinsic model to be the eigenspace of C, associated with the maximal eigenvalue; that is,

$$\mathbb{V} = \mathcal{H}(\lambda_{\max}).$$

There are two immediate implications of Theorem 5. The first implication is that vector space $\mathbb{V}$ is three dimensional. The second implication is that there exists a spectral gap of $\lambda_1 - \lambda_3 = 5/12$ that separates the maximal eigenvalue $\lambda_{\max}$ from the rest of the spectrum.

Let $\tau : V \to \mathcal{H}$ be the map sending a vector $v \in V$ to the section $\tau(v) \in \mathcal{H}$, given by

$$\tau(v)(x) = \sqrt{3/2} \cdot \mathrm{pr}_x(v),$$

where pr_x is the orthogonal projection onto the plane $x^\perp$. The first claim is, that the image of the map τ coincides with the subspace $\mathbb{V} \subset \mathcal{H}$, and, moreover, that the map τ induces an isometry onto its image.

In addition, let us define the morphism

$$\varphi_x = \sqrt{2/3} \cdot (\mathrm{ev}_x|\mathbb{V})^t : x^\perp \to \mathbb{V}$$

for every $x \in S(V)$, where $\mathrm{ev}_x : \mathcal{H} \to x^\perp$ is the evaluation morphism at the point $x \in S(V)$. The second claim is that the morphism τ satisfies

$$\tau \circ i_x = \varphi_x$$

for every $x \in S(V)$. These two claims in conjunction establish the content of the following theorem.

THEOREM 6. *The morphism τ maps V isometrically onto $\mathbb{V}$. Moreover,*

$$\tau \circ i_x = \varphi_x$$

for every $x \in S(V)$.

For a proof, see Appendix A. The proof is based on interpreting the spectrum of the common lines operator in terms of the representation theory of the orthogonal group acting on the vector space $\mathcal{H}$. The proof uses the results and terminology of Section 2.

2. **Spectral analysis of the common lines operator**

This section constitutes the main technical part of the paper. Our goal in this section is to interpret the spectrum of the common lines operator in terms of the representation theory of the orthogonal group $O(V)$ acting on the vector space $\mathcal{H}$. As a consequence, we obtain a proof of Theorem 5.

2.1. *Set-up.* It will be convenient to extend the set-up a bit.

2.1.1. *Auxiliary vector bundles and their complexifications.* In addition to the vector bundle of planes $\mathfrak{H}$, we introduce two auxiliary vector bundles on the unit sphere $S(V)$: the vector bundle of normal lines $\mathfrak{N} \to S(V)$, with fibers $\mathfrak{N}_{|x} = \mathbb{R}x$ and the trivial vector bundle $V_{S(V)}$ with fiber at each point equal to V. We denote the vector space of smooth global sections of $\mathfrak{N}$ by $\mathcal{N}$ and that of $V_{S(V)}$ by $\mathcal{V}$, noting that $\mathcal{V} = \mathcal{F} \otimes V$, where $\mathcal{F} = C^\infty(S(V), \mathbb{R})$. In addition, we have

$$\mathcal{V} = \mathcal{H} \oplus \mathcal{N}.$$

Both vector bundles are equipped with a fiberwise Euclidean structure which is induced from the one on V; consequently, the spaces of global sections carry a Euclidean inner product. In addition, all the vector bundles are equipped with a natural $O(V)$-equivariant structure, compatible with the Euclidean structure and consequently the spaces of global sections carry an action of the group $O(V)$, preserving the Euclidean structure. It is convenient to split the action of the full orthogonal group to an action of the special orthogonal

group $\mathrm{SO}(V)$, supplemented with a commuting action of the special element $\omega \in O(V)$.

We also consider the complexified vector bundles $\mathbb{C}\mathfrak{H}, \mathbb{C}\mathfrak{N}$ and $\mathbb{C}V_{S(V)}$ as well as their corresponding vector spaces of smooth global sections $\mathbb{C}\mathcal{H}, \mathbb{C}\mathcal{N}$ and $\mathbb{C}\mathcal{V}$. These vector bundled are equipped with a fiberwise Hermitian inner product induced from the Hermitian product h on $\mathbb{C}V$, given by

$$h(u,v) = r(\overline{u}, v),$$

where $\overline{(-)} : \mathbb{C}V \to \mathbb{C}V$ is complex conjugation. Consequently, the vector spaces of smooth global sections are a (pre) Hermitian vector spaces carrying a unitary representation of the group $O(V)$.

2.1.2. *The operator of orthographic lines.* We define an integral operator $O : \mathcal{H} \to \mathcal{H}$, referred to as the *operator of orthographic lines*. This operator captures another basic relation in three dimensional Euclidean geometry which stands in duality with the common line relation.

The orthographic lines operator is defined by the following kernel. For every pair of points $x, y \in S(V)$ in generic position, let us consider the corresponding unit vectors

$$o_{x,y} = \frac{\mathrm{pr}_x(y)}{\|\mathrm{pr}_x(y)\|} \in x^{\perp},$$

$$o_{y,x} = \frac{\mathrm{pr}_y(x)}{\left\|\mathrm{pr}_y(x)\right\|} \in y^{\perp}.$$

The vector $o_{x,y}$ is the normalized projection of the vector y on the plane $x^{\perp}$ and similarly the vector $o_{y,x}$ is the normalized projection of the vector x on the plane $y^{\perp}$. We define a rank one operator $O(x,y) : y^{\perp} \to x^{\perp}$ by

$$O(x,y)(v) = r(o_{y,x}, v)\, o_{x,y}$$

for every $v \in y^{\perp}$. The collection $\{O(x,y) : x, y \in X \text{ in generic position}\}$ defines a distribution section of $\mathfrak{H} \boxtimes \mathfrak{H}^*$ that is smooth on the complement of the union of the diagonal and the anti-diagonal that, in turn, yields an integral operator $O : \mathcal{H} \to \mathcal{H}$. In addition,

- the orthographic lines operator is symmetric, since $O(x,y) = O(y,x)^t$ for every $x, y \in X$ in generic position;
- the orthographic lines operator commutes with the $O(V)$-action, since $O(gx, gy) = g \circ O(x,y) \circ g^{-1}$ for every $x, y \in X$ in generic position and $g \in O(V)$.

Finally, it is not difficult to verify that, for any pair of points $x, y \in S(V)$ in generic position, the orthographic lines $\mathbb{R}o_{x,y} \subset x^{\perp}$ and $\mathbb{R}o_{y,x} \subset y^{\perp}$ are orthogonal to the common line $x^{\perp} \cap y^{\perp}$ and the linear map $O(x,y)$ satisfy

$O(x,-y) = O(-x,y) = -1 \cdot O(x,y)$. The latter property implies that the orthographic line map $O(x,y)$ depends on the choice of the unit vectors x, y, in contrast to the common line map $C(x,y)$ which depends only on the planes $x^\perp, y^\perp$.

2.1.3. *The operator of parallel translation.* We define the integral operator $T = C - O : \mathcal{H} \to \mathcal{H}$, referred to as the operator of *parallel translations*.

It is not difficult to verify that the kernel $T(x,y) : y^\perp \to x^\perp$ for every pair of points $x, y \in S(V)$ in generic position is an orthogonal linear map that coincides with parallel translation along the unique geodesic (large circle) connecting the point y with the point x.

The parallel transport operator is symmetric and commutes with the $O(V)$-action, since both the common lines operator and the orthographic lines operator satisfy these properties.

The strategy that we are going to follow is to study the spectral properties of the operator T, from which, as it turns out, the spectral properties of the operators C and O can be derived.

2.2. *Isotypic decompositions.* The spaces $\mathcal{H}, \mathcal{V}, \mathcal{N}$ and $\mathcal{F}$ carry an action of the group $\mathrm{SO}(V)$, preserving the Euclidean structure. As such, they admit isotypic decomposition[3]

$$\mathcal{H} = \bigoplus_{n=0}^{\infty} \mathcal{H}_n,\ \mathcal{N} = \bigoplus_{n=0}^{\infty} \mathcal{N}_n,$$
$$\mathcal{V} = \bigoplus_{n=0}^{\infty} \mathcal{V}_n,\ \mathcal{F} = \bigoplus_{n=0}^{\infty} \mathcal{F}_n,$$

where we use the subscript n to denote the isotypic component associated with the unique irreducible representation of $\mathrm{SO}(V)$ of dimension $2n+1$. In addition, the element $\omega \in O(V)$ acts on all these vector spaces, thus decomposing them into direct sum of two components

$$\mathcal{H} = \mathcal{H}^+ \oplus \mathcal{H}^-,\ \mathcal{N} = \mathcal{N}^+ \oplus \mathcal{N}^-,$$
$$\mathcal{V}_n = \mathcal{V}^+ \oplus \mathcal{V}^-,\ \mathcal{F} = \mathcal{F}^+ \oplus \mathcal{F}^-,$$

where we use the superscript $+$ to denote the component on which ω acts as Id and the superscript $-$ to denote the component on which ω acts as $-\mathrm{Id}$. We will refer to the $+$ component as the *symmetric* component and to the $-$ component as the *anti-symmetric* component. The following theorem summarizes the properties of these decompositions.

[3]We remind the reader that an isotypic component is a representation which is a direct sum of copies a single irreducible representation.

THEOREM 7. *The following properties hold.*

(1) *Each isotypic component $\mathcal{F}_n$ is an irreducible representation. Moreover, $\mathcal{F}_n = \mathcal{F}_n^+$ when n is even and $\mathcal{F}_n = \mathcal{F}_n^-$ when n is odd.*
(2) *Each isotypic component $\mathcal{N}_n$ is an irreducible representation. Moreover, $\mathcal{N}_n = \mathcal{N}_n^+$ when n is even and $\mathcal{N}_n = \mathcal{N}_n^-$ when n is odd.*
(3) *The isotypic component $\mathcal{H}_0 = 0$ and each isotypic component $\mathcal{H}_n$, $n \geq 1$ decomposes under ω into a direct sum of two irreducible representations $\mathcal{H}_n^+ \oplus \mathcal{H}_n^-$.*
(4) *The isotypic component $\mathcal{V}_0$ is equal to the symmetric trivial representation $\mathbf{1}^+$ and each isotypic component $\mathcal{V}_n$, $n \geq 1$ decomposes under ω into a direct sum of three irreducible representations $\mathcal{H}_n^+ \oplus \mathcal{H}_n^- \oplus \mathcal{N}_n^?$ where*

$$? = \begin{cases} + & n \text{ even} \\ - & n \text{ odd.} \end{cases}$$

For a proof, see Appendix A.

Since the operators C, O and T commute with the $O(V)$-action, they preserve all the above decompositions.

PROPOSITION 1. *The following properties hold.*

- *The operator T acts as scalar operator on $\mathcal{H}_n$; moreover, $T|\mathcal{H}_n = \lambda_n \mathrm{Id}$ where $\lambda_n \neq 0$.*
- *The isotypic component $\mathcal{H}_n^+ \subset \ker C$; moreover, $C|\mathcal{H}_n^- = \lambda_n \mathrm{Id}$.*
- *The isotypic component $\mathcal{H}_n^- \subset \ker O$; moreover, $O|\mathcal{H}_n^+ = -\lambda_n \mathrm{Id}$.*

For a proof, see Appendix A.

The rest of this section is devoted to the computation of the eigenvalues λ_n, $n \geq 1$.

2.3. *Computation of the eigenvalues.* Fix a point $x \in S(V)$. Let $T_x = \{g \in \mathrm{SO}(V) : gx = x\}$ be the subgroup of rotations around x. Choose an sl_2 triple $(H, E, F) \in \mathbb{C}\,\mathrm{Lie}(\mathrm{SO}(V))$ associated with T_x.

2.3.1. *Spherical decomposition.* For each $n \geq 1$, the complexified (Hilbert) space $\mathbb{C}\mathcal{H}_n$ admits an isotypic decomposition into weight spaces with respect to the action of the elements H

$$\mathbb{C}\mathcal{H}_n = \bigoplus_{m=-n}^{n} \mathbb{C}\mathcal{H}_n^m,$$

where H acts on $\mathbb{C}\mathcal{H}_n^m$ by $2m\mathrm{Id}$. Since $\mathbb{C}\mathcal{H}_n = \mathbb{C}\mathcal{H}_n^+ \oplus \mathbb{C}\mathcal{H}_n^-$, each weight space $\mathbb{C}\mathcal{H}_n^m$ is two-dimensional. Given a section $u_n \in \mathbb{C}\mathcal{H}_n$, by Proposition 1, $Tu_n = \lambda_n u_n$. If, in addition, $u_n(x) \neq 0$, then the eigenvalue λ_n can be computed from the equation

$$\lambda_n \cdot h(u_n(x), u_n(x)) = h(u_n(x), Tu_n(x)). \tag{2.1}$$

Let us fix a unit vector $l_0 \in x^{\perp}$ and consider an infinitesimal generator $A_{l_0} \in \mathrm{Lie}\left(T_{l_0}\right)$, satisfying the property that the exponential mapping $\exp : [0, 2\pi) \to T_{l_0}$, $\exp(\theta) = e^{\theta A_{l_0}}$ is a diffeomorphism. The following proposition establishes an integral formula for the right-hand side of equation (2.1) expressed in terms of the exponential mapping $\exp : [0, 2\pi) \to T_{l_0}$.

PROPOSITION 2. *Assume $u_n \in \mathbb{C}\mathcal{H}_n^1$; then*

$$\lambda_n \cdot h\left(u_n(x), u_n(x)\right) = \int_0^{\pi} \mu(\theta)\, h\left(u_n(x), e^{-\theta A_{l_0}} u_n\left(e^{\theta A_{l_0}} x\right)\right) d\theta, \tag{2.2}$$

where $\mu(\theta) = \sin(\theta)/2$.

For a proof, see Appendix A.

2.3.2. *Construction of a "good" section.* Our strategy is to construct a section $u_n \in \mathbb{C}\mathcal{H}_n^1$, satisfying $u_n(x) \neq 0$, and then, to use equation (2.2) in order to compute the eigenvalue λ_n. To this end, we choose a highest weight vector $\psi_n \in \mathbb{C}\mathcal{F}_n$ (i.e., $H\psi_n = 2n\psi_n$) for every $n \geq 0$ and a highest weight vector $v_1 \in \mathbb{C}V$ ($Hv_1 = 2v_1$). Consequently, the section $\psi_{n-1} \otimes v_1$ is a highest weight vector in $\mathbb{C}\mathcal{V}_n$ for every $n \geq 1$.

We construct the section u_n in two steps. In the first step, we apply the lowering operator F and consider the section $\widetilde{u}_n = F^{n-1}\left(\psi_{n-1} \otimes v_1\right) \in \mathbb{C}\mathcal{V}_n^1$. In the second step, we project $\widetilde{u}_n$ onto $\mathbb{C}\mathcal{H}_n$, by taking

$$u_n(y) = \mathrm{pr}_y \widetilde{u}_n(y)$$

for every $y \in S(V)$, where pr_y is the orthogonal projection operator on $\mathbb{C}y^{\perp}$.

PROPOSITION 3. *The section u_n is symmetric or anti-symmetric depending on the parity of n as follows*:

$$u_n \in \mathbb{C}\mathcal{H}_n^{+,1} \text{ when } n \text{ is even}, \qquad u_n \in \mathbb{C}\mathcal{H}_n^{-,1} \text{ when } n \text{ is odd}.$$

For a proof, see Appendix A.

Let us denote by P_{n-1} the weight zero spherical function $F^{n-1}\psi_{n-1} \in \mathcal{F}_{n-1}^0$. The following proposition gives an explicit expression of $\widetilde{u}_n$ in terms of the function P_{n-1} and the vector v_1.

PROPOSITION 4. *The section $\widetilde{u}_n$ can be written as*

$$\widetilde{u}_n = P_{n-1} \otimes v_1 + \frac{1}{n} EP_{n-1} \otimes Fv_1 + \frac{1}{2n(n+1)} E^2 P_{n-1} \otimes F^2 v_1. \tag{2.3}$$

For a proof, see Appendix A.

We are now ready to finish the computation of the eigenvalue. Using equation (2.2), we can write

$$\lambda_n \cdot h\left(u_n(x), u_n(x)\right) = \int_0^{\pi} \mu(\theta)\, h\left(e^{\theta A_{l_0}} u_n(x), \widetilde{u}_n\left(e^{\theta A_{l_0}} x\right)\right) d\theta.$$

Considering formula (2.3), it is evident that the functions EP_{n-1} and E^2P_{n-1} must vanish at $x \in S(V)$ since these are functions of weight different from zero with respect to the action of T_x. Hence

$$u_n(x) = \widetilde{u}_n(x) = P_{n-1}(x)\, v_1 \in \mathbb{C}x^{\perp,1}.$$

For $k = 0, 1, 2$, let us define the integrals

$$\begin{aligned} I_n^k &= \frac{1}{h(u_n(x), u_n(x))} \int_0^\pi \mu(\theta)\, h\left(e^{\theta A_{l_0}} u_n(x), E^k P_{n-1}\left(e^{\theta A_{l_0}} x\right) F^k v_1\right) d\theta \\ &= \frac{1}{P_{n-1}(x)\, h(v_1, v_1)} \int_0^\pi \mu(\theta)\, E^k P_{n-1}\left(e^{\theta A_{l_0}} x\right) h\left(e^{\theta A_{l_0}} v_1, F^k v_1\right) d\theta. \end{aligned}$$

The eigenvalue λ_n can be expressed as

$$\lambda_n = I_n^0 + \frac{1}{n} I_n^1 + \frac{1}{2n(n+1)} I_n^2. \tag{2.4}$$

THEOREM 8 (Main technical statement). *For $k = 0, 1, 2$, the integrals I_n^k are equal to*

$$I_n^0 = \begin{cases} 1 & n = 1 \\ 1/6 & n = 2 \\ 0 & n \geq 3 \end{cases},$$

$$I_n^1 = \begin{cases} 0 & n = 1 \\ -2/3 & n = 2 \\ 0 & n \geq 3 \end{cases},$$

$$I_n^2 = \begin{cases} 0 & n = 1 \\ 0 & n = 2 \\ 2(-1)^{n-1} & n \geq 3 \end{cases}.$$

For a proof, see Section 2.4.

Using Theorem 8 and equation (2.4) we obtain the desired formula

$$\lambda_n = \frac{(-1)^{n-1}}{n(n+1)},$$

which proves Theorem 5.

2.4. *Proof of Theorem* 8.

2.4.1. *Set-up.* Let (e_1, e_2, e_3) be an orthonormal basis of V. Think of the basis vector e_3 as playing the role of the fixed unit vector $x \in S(V)$, and of the basis vector e_2 as playing the role of the vector $l_0 \in S\left(x^\perp\right)$. It is possible

to choose elements $A_{e_i} \in \mathrm{Lie}\,(T_{e_i})$, $i = 1, 2, 3$, that satisfy the relations

$$\begin{aligned}[A_{e_3}, A_{e_1}] &= A_{e_2},\\ [A_{e_3}, A_{e_2}] &= -A_{e_1},\\ [A_{e_1}, A_{e_2}] &= A_{e_3},\end{aligned}$$

and, in addition, satisfy $\left[A_{e_i}, A_{e_j}\right] = A_{e_i e_j}$ for every $1 \le i, j \le 3$. We consider the following sl_2 triple (H, E, F) associated with T_{e_3}:

$$\begin{aligned}H &= -2iA_{e_3},\\ E &= iA_{e_2} - A_{e_1},\\ F &= A_{e_1} + iA_{e_2}.\end{aligned}$$

We introduce spherical coordinates $f : (0, 2\pi) \times (0, \pi) \to S(V)$ given by $f(\varphi, \theta) = g_\varphi \cdot (\cos(\theta)\, e_3 + \sin(\theta)\, e_1)$, where

$$g_\varphi = \begin{pmatrix} \cos(\varphi) & -\sin(\varphi) & 0\\ \sin(\varphi) & \cos(\varphi) & 0\\ 0 & 0 & 1\end{pmatrix}.$$

In the coordinates (φ, θ), the operators H, E, F are given by the following formulas:

$$\begin{aligned}H &= 2i\partial_\varphi,\\ E &= -e^{-i\varphi}\left(i\partial_\theta + \cot(\theta)\,\partial_\varphi\right),\\ F &= -e^{i\varphi}\left(i\partial_\theta - \cot(\theta)\,\partial_\varphi\right).\end{aligned}$$

2.4.2. *Highest weight vector in V.* The vector $v_1 = -e_1 + ie_2$ is a highest weight vector in V, and we note that $\|v_1\|^2 = 2$. For $k = 0, 1, 2$, let us denote by $j^k(\theta)$ the function $\left\langle e^{\theta A_{e_2}} v_1, F^k v_1\right\rangle$. Explicit calculation shows that

$$\begin{aligned}j^0(\theta) &= \cos(\theta) + 1,\\ j^1(\theta) &= 2i\sin(\theta),\\ j^2(\theta) &= 2\cos(\theta) - 2.\end{aligned}$$

2.4.3. *Spherical function in $\mathcal{F}_n$.* For every $n \ge 0$, let $P_n \in \mathcal{F}_n^0$ denote the unique weight zero spherical function, satisfying the normalization condition $P_n(e_3) = 1$. Define the generating function

$$G(\varphi, \theta, t) = \sum_{n=0}^{\infty} P_n(\varphi, \theta)\, t^n.$$

The generating function G admits an explicit formula.

Theorem 9 ([11]).

$$G(\varphi, \theta, t) = \left(1 - 2t\cos(\theta) + t^2\right)^{-1/2}. \tag{2.5}$$

Remark 3. Note that $G(0,0,t) = (1-t)^{-1} = \sum_{n=0}^{\infty} t^n$ which is compatible with the normalization condition $P_n(0,0) = 1$.

Applying the raising operator E, we obtain the generating functions

$$EG(\varphi,\theta,t) = \sum_{n=0}^{\infty} EP_n(\varphi,\theta)\, t^n,$$
$$E^2G(\varphi,\theta,t) = \sum_{n=0}^{\infty} E^2P_n(\varphi,\theta)\, t^n.$$

Granting formula (2.5), explicit calculation gives

$$EG(\varphi,\theta,t) = ie^{-i\varphi}t\sin(\theta)\left(1-2t\cos(\theta)+t^2\right)^{-3/2},$$
$$E^2G(\varphi,\theta,t) = -3e^{-2i\varphi}t^2\sin^2(\theta)\left(1-2t\cos(\theta)+t^2\right)^{-5/2}.$$

2.4.4. *Putting everything together.* In terms of our choice of the highest weight vector v_1 and the spherical functions P_n, $n \geq 0$, the integrals I_n^k, $k = 0,1,2$, can be written in the spherical coordinates (φ,θ) as

$$I_n^k = \frac{1}{P_{n-1}(x)\, h(v_1,v_1)} \int_0^{\pi} \mu(\theta)\, E^k P_{n-1}(0,\theta)\, j^k(\theta)\, d\theta$$
$$= \frac{1}{2} \int_0^{\pi} \mu(\theta)\, E^k P_{n-1}(0,\theta)\, j^k(\theta)\, d\theta.$$

For $k = 0,1,2$, define the generating functions

$$I^k(t) = \sum_{n=0}^{\infty} I_{n+1}^k t^n.$$

Each $I^k(t)$ can be expressed as the integral

$$I^k(t) = \frac{1}{2} \int_0^{\pi} \mu(\theta)\, E^k G(0,\theta,t)\, j^k(\theta)\, d\theta.$$

Explicit calculation of the integrals $I^k(t)$ shows that

$$I^0(t) = \frac{1}{2}\left(1+\frac{1}{3}t\right),$$
$$I^1(t) = \frac{1}{2}\left(-\frac{4}{3}t\right),$$
$$I^2(t) = \frac{1}{2}\left(4(1+t)^{-1} - 4t - 4\right) = 2\sum_{n=2}^{\infty}(-1)^n t^n.$$

From the above formulas, using equation (2.4), we obtain

$$\lambda_n = \frac{(-1)^{n-1}}{n\,(n+1)}$$

for every $n \geq 1$. This concludes the proof of Theorem 8.

Appendix A. Proofs

A.1. *Proof of Theorem* 6. Since τ is a morphism of $O(V)$ representations, it maps V isometrically onto $\mathcal{H}_1^-$ — the unique anti-symmetric copy (ω acts by -1) of the three dimensional representation of $\mathrm{SO}(V)$, which, by Proposition 1, coincides with $\mathbb{V} = \mathcal{H}(\lambda_{\max})$. Evidently, τ is an isometry, up to a scalar; hence, it is sufficient to show that $\mathrm{Tr}\left(\tau \circ \tau^t\right) = 3$. We let $\alpha : V \to \mathcal{H}$ denote the morphism defined by

$$\alpha(v)(x) = \mathrm{pr}_x(v)$$

for every $v \in V$ and $x \in S(V)$. Note that $\tau = \sqrt{3/2} \cdot \alpha$. We have

$$\begin{aligned}\mathrm{Tr}\left(\tau \circ \tau^t\right) &= \frac{3}{2} \cdot \mathrm{Tr}\left(\alpha \circ \alpha^t\right) = \frac{3}{2} \int\limits_{x \in S(V)} \mathrm{Tr}\left(i_x^t \circ i_x\right) dx \\ &= \frac{3}{2} \int\limits_{x \in S(V)} 2dx = 3.\end{aligned}$$

Finally, the relation $\tau \circ i_x = \varphi_x$ follows from

$$(\mathrm{ev}_x | \mathbb{V}) \circ \alpha = \mathrm{pr}_x$$

for every $x \in X$. This concludes the proof of the theorem.

A.2. *Proof of Theorem* 7. Property 1 is the classical result of spherical harmonics on the two dimensional sphere; see, e.g., [11]. We just note that the representation $\mathcal{F}_n$ consists of the restriction to $S(V)$ of harmonic polynomials of degree n, which implies that $\mathcal{F}_n = \mathcal{F}_n^+$ when n is even and $\mathcal{F}_n = \mathcal{F}_n^-$ when n is odd.

Property 2 follows from Property 1 since $\mathcal{N}$ can be trivialized using the $O(V)$-invariant section $s \in \mathcal{N}$, defined by $s(y) = y$ for every $y \in S(V)$.

We now prove Properties 3 and 4 simultaneously.

Since $\mathcal{V} = \mathcal{F} \otimes V$ as a representation of $O(V)$, we can express the isotypic components of $\mathcal{V}$ in terms of the isotypic components of $\mathcal{F}$ as follows.

- For $n = 0$, $\mathcal{F}_0 \otimes V = V^-$.
- For $n \geq 1$, $\mathcal{F}_n \otimes V = (\mathcal{F}_n \otimes V)^?_{n-1} \oplus (\mathcal{F}_n \otimes V)^?_n \oplus (\mathcal{F}_n \otimes V)^?_{n+1}$, where

$$? = \begin{cases} + & n \text{ odd} \\ - & n \text{ even.} \end{cases}$$

The decomposition of $\mathcal{F}_n \otimes V$ as a representation of $\mathrm{SO}(V)$ is computed using the branching rules of a tensor product, and the action of $\omega \in O(V)$ is derived from the facts that $V = V^-$ and Property 1.

This implies that the isotypic components of $\mathcal{V}$ are:

- for $n = 0$, $\mathcal{V}_n = \mathbf{1}^+$;
- for odd $n \geq 1$, $\mathcal{V}_n = (\mathcal{F}_{n-1} \otimes V)^-_n \oplus (\mathcal{F}_n \otimes V)^+_n \oplus (\mathcal{F}_{n+1} \otimes V)^-_n$;
- for even $n \geq 1$, $\mathcal{V}_n = (\mathcal{F}_{n-1} \otimes V)^+_n \oplus (\mathcal{F}_n \otimes V)^-_n \oplus (\mathcal{F}_{n+1} \otimes V)^+_n$.

Combining this with Property 2 and the fact that $\mathcal{V} = \mathcal{H} \oplus \mathcal{N}$ yields Properties 3 and 4.

This concludes the proof of the theorem.

A.3. *Proof of Proposition* 1. Fix $n \geq 1$. Denote $\mathcal{H} = \mathcal{H}_n$ and $\mathcal{H}^\pm = \mathcal{H}^\pm_n$.

The statement that $\mathcal{H}^+ \subset \ker C$ follows from $C(x,-y) = C(-x,y) = C(x,y)$ in conjunction with the fact that a section $s \in \mathcal{H}^+$ satisfies $s(-x) = -(\omega \cdot s)(x) = -s(x)$. Similarly, the statement that $\mathcal{H}^- \subset \ker O$ follows from $O(x,-y) = O(-x,y) = -O(x,y)$ in conjunction with the fact that a section $s \in \mathcal{H}^-$ satisfies $s(-x) = -(\omega \cdot s)(x) = s(x)$.

Since, by definition, $T = C - O$, this implies that $C_{|\mathcal{H}^-} = T_{|\mathcal{H}^-}$ and $-O|\mathcal{H}^+ = T|\mathcal{H}^+$. Since T commutes with the action of $\mathrm{SO}(V)$ and $\mathcal{H}^\pm$ are irreducible representations,

$$T|\mathcal{H}^\pm = \lambda^\pm \mathrm{Id}.$$

We are left to show that $\lambda^+ = \lambda^-$. The argument proceeds as follows. Let us denote by $\mathrm{ev}_x : \mathbb{C}\mathcal{H} \to \mathbb{C}x^\perp$ the evaluation map at the point x. Since x is fixed by the group T_x, this implies that ev_x is a morphism of representations of T_x. Moreover, ev_x induces an isomorphism of weight spaces $\mathrm{ev}_x : \mathbb{C}\mathcal{H}^{\pm,1} \xrightarrow{\simeq} \mathbb{C}x^{\perp,1}$. Fix sections $u^\pm \in \mathbb{C}\mathcal{H}^{\pm,1}$ normalized to be of norm 1. Applying Formula (2.2)), we can write

$$\begin{aligned} \lambda^\pm h\left(\mathrm{ev}_x u^\pm, \mathrm{ev}_x u^\pm\right) &= \int_0^\pi \mu(\theta)\, h\left(\mathrm{ev}_x u^\pm, \mathrm{ev}_x\left(e^{\theta A_{l_0}} u^\pm\right)\right) d\theta \\ &= h\left(\mathrm{ev}_x u^\pm, \mathrm{ev}_x\left(\pi^\pm(\overline{\mu})\, u_n\right)\right), \end{aligned} \tag{A.1}$$

where $\pi^\pm : T_x \to U(\mathbb{C}\mathcal{H}^\pm)$ are the group actions restricted to the subgroup T_x and $\overline{\mu}$ is the function on T_x corresponding to μ via the isomorphism $e^{\theta A_{l_0}}$.

Equation (A.1) implies that $\lambda^\pm = \langle u^\pm, \pi^\pm(\overline{\mu})\, u^\pm \rangle_{\mathbb{C}\mathcal{H}^\pm}$. This implies that $\lambda^\pm$ are characterized solely in terms of the irreducible representation $\pi^\pm : \mathrm{SO}(V) \to U(\mathbb{C}\mathcal{H}^\pm)$, which, in turns, implies that $\lambda^+ = \lambda^-$.

This concludes the proof of the proposition.

A.4. *Proof of Proposition* 2. Let $f : T_x \times (0,\pi) \to S(V)$ be the spherical coordinates on $S(V)$ given by $f(g,\theta) = g e^{\theta A_{l_0}} x$. In these coordinates, the

normalized Haar measure on $S(V)$ is given by $dg \boxtimes \mu(\theta)\, d\theta$, where dg is the normalized Haar measure on T_x and $\mu(\theta) = \sin(\theta)/2$.

The section $u_n \in \mathbb{C}\mathcal{H}_n^1$ is a character vector with respect to the group T_x. Let us denote this character by $\chi : T_x \to S^1$ and note that we have $g \cdot u_n = \chi(g)\, u_n$ for every $g \in T_x$. Now, compute

$$\begin{aligned}
\lambda_n h(u_n(x), u_n(x)) &= h(u_n(x), Tu_n(x)) \\
&= \int_{y \in S(V)} h(u_n(x), T(x,y)\, u_n(y))\, dy \\
&= \int_{T_x} dg \int_0^\pi \mu(\theta)\, h\left(u_n(x), T\left(x, ge^{\theta A_{l_0}} x\right) u_n\left(ge^{\theta A_{l_0}} x\right)\right) d\theta \\
&= \int_{T_x} dg \int_0^\pi \mu(\theta)\, h\left(u_n(x), gT\left(x, e^{\theta A_{l_0}} x\right) g^{-1} u_n\left(ge^{\theta A_{l_0}} x\right)\right) d\theta \\
&= \int_{T_x} dg \int_0^\pi \mu(\theta)\, h\left(g^{-1}u_n(x), T\left(x, e^{\theta A_{l_0}} x\right) g^{-1} u_n\left(ge^{\theta A_{l_0}} x\right)\right) d\theta \\
&= \int_{T_x} dg \int_0^\pi \mu(\theta)\, h\left(u_n(x), T\left(x, e^{\theta A_{l_0}} x\right) u_n\left(e^{\theta A_{l_0}} x\right)\right) d\theta \\
&= \int_0^\pi \mu(\theta)\, h\left(u_n(x), e^{-\theta A_{l_0}} u_n\left(e^{\theta A_{l_0}} x\right)\right) d\theta,
\end{aligned}$$

where Step 4 uses that T commutes with the action of $\mathrm{SO}(V)$, which is equivalent to the property that $T(gx, gy) = g \circ T(x,y) \circ g^{-1}$ for every $x, y \in S(V)$ and $g \in \mathrm{SO}(V)$. In particular, this implies that $T\left(x, ge^{\theta A_{l_0}} x\right) = T\left(gx, ge^{\theta A_{l_0}} x\right) = g \circ T\left(x, e^{\theta A_{l_0}} x\right) \circ g^{-1}$. Step 7 in the derivation uses that $T\left(x, e^{\theta A_{l_0}} x\right)$ is the operator of parallel translation along the big circle connecting the point $e^{\theta A_{l_0}} x$ with the point x.

This concludes the proof of the proposition.

A.5. *Proof of Proposition* 4. First we note the following simple fact: the operator $EF\colon \mathbb{C}\mathcal{V}_n \to \mathbb{C}\mathcal{V}_n$ preserves the weight spaces $\mathbb{C}\mathcal{V}_n^l$. Moreover, since $\mathbb{C}\mathcal{V}_n$ is a representation of highest weight $2n$ with respect to the sl_2 triple (H, E, F), we have

$$EF|\mathbb{C}\mathcal{V}_n^l = (n+l)(n-l+1)\,\mathrm{Id}, \tag{A.2}$$

for $l = -n, \ldots, n$. Now, calculate

$$\widetilde{u}_n = F^{n-1}(\psi_{n-1} \otimes v_1) = \sum_{i=0}^{n-1} \binom{n-1}{i} F^{n-1-i} \otimes F^i (\psi_{n-1} \otimes v_1).$$

Since $\mathbb{C}V$ is a representation of highest weight 2 with respect to the sl_2 triple (H, E, F), all tensors of the form $(-) \otimes F^k v_1$, for $k \geq 3$, vanish. This implies that the above sum is equal to

$$F^{n-1}\psi_{n-1} \otimes v_1 + (n-1)\, F^{n-2}\psi_{n-1} \otimes F v_1 + \frac{(n-1)\,(n-2)}{2} F^{n-3}\psi_{n-1} \otimes F^2 v_1.$$

Recall that $P_{n-1} = F^{n-1}\psi_{n-1}$. Explicit calculation, using formula (A.2), shows that

$$F^{n-1}\psi_{n-1} = \frac{1}{n\,(n-1)} E P_{n-1},$$
$$F^{n-3}\psi_{n-1} = \frac{1}{(n-2)\,(n-1)\,n\,(n+1)} E^2 P_{n-1}.$$

Combining all the above yields the desired formula for $\widetilde{u}_n$.

This concludes the proof of the proposition.

A.6. *Proof of Proposition* 3. The statement follows directly from the facts that $V = V^-$ which implies that $\omega\left(F^k v_1\right) = -F^k v_1$ and that $P_{n-1} \in \mathcal{F}^?_{n-1}$, where

$$? = \begin{cases} + & n \text{ odd} \\ - & n \text{ even.} \end{cases}$$

This concludes the proof of the proposition.

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(Received: October 14, 2009)

The University of Texas at Austin, Austin, TX
E-mail: hadani@math.utexas.edu

Department of Mathematics and PACM, Princeton University, Princeton, NJ
E-mail: amits@math.princeton.edu